The impacts of street lighting on bats

Submitted by Julie Day to the University of Exeter

as a thesis for the degree of

Doctor of Philosophy in Biological Sciences

In June 2017

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: ……..

Abstract

As human population grows and develops, more urban areas are expanding. Urbanisation has many impacts on the natural environment and one understudied pollutant is artificial light at night. The aims of this thesis were to examine the impacts of street lighting on bats and investigate the exposure of British bat species to artificial light at night and explored the mitigation option of part-night lighting.

The current exposure of British bat species to artificial lighting was assessed using roost locations and population sizes from a long-term dataset (1997–2012) from the Bat Conservation Trust's National Bat Monitoring Programme on seven bat species (*Eptesicus serotinus*, *Myotis nattereri*, *Pipistrellus pipistrellus*, *P. pygmaeus*, *Plecotus auritus, Rhinolophus hipposideros* and *R. ferrumequinum*). These data were combined with satellite imagery in roost sustenance zones and home ranges. Bat roosts were found in areas with brighter light levels than random locations for *P. pipistrellus*, *P. pygmaeus* and *Plecotus auritus*. Species that forage around streetlights (*P. pipistrellus* and *P. pygmaeus*) had significantly higher light levels in the landscape around their roosts than species which avoid street lit areas (*R. hipposideros, M. nattereri* and *P. auritus*). Colony size was negatively correlated with light levels. This study highlights that different species have different requirements in the landscapes around their roosts.

To investigate landscapes effects of artificial light at night on the understudied light avoiding species *R. ferrumequinum*, eight maternity roosts were surveyed to explore the interaction between habitat features and street lighting. At each maternity roost,

bat detectors were deployed at 25 paired street lit and dark locations. Street lighting had a significant negative effect on bat activity. Locations closest to the maternity roost had higher bat activity than those further away and road type had a significant effect on bat activity, with the highest bat activity recorded at minor roads compared with A and B roads. These results highlight the large negative impact street lighting can have on bat activity patterns and the need for mitigation.

Several mitigation strategies have been suggested to combat the effects of artificial light at night but few have been tested. One of these suggestions is to restrict the hours of lighting through the night, often called part-night lighting. Part-night lighting has been implemented by many local authorities, often switching the lights off after midnight and switching them back on before dusk. To explore the effects of part-night lighting on bats, the hourly patterns of activity for *R. ferrumequinum* were studied. Bat activity was bimodal, with a peak in the first few hours after sunset followed by a smaller peak before sunrise. To capture more than 50% of bat activity during the dark period of the night, street lights would be required to switch off before 11pm. To explore this further, a before-and-after study of part-night lighting was conducted at towns across Devon. Following the conversion from full-night lighting to part-night lighting, switching street lights off at 2 am, there was a significant reduction in *P. pipistrellus* and a significant increase for *P. pygmaeus* and *Nyctalus noctule* activity. Although part-night lighting is not often operational during peak activity periods for bat species, reducing the duration of lighting at night has impacts on activity patterns for several species.

This thesis shows that artificial light at night has impacts on bats across the landscapes around their roosts. Artificial lighting has impacts for species in different ways, depending on whether they forage around street lights or avoid street lit areas. For species that avoid street lit areas such as *R. ferrumequinum*, street lighting can have very significant negative impacts on the availability of areas around their roosts. This highlights the need for conservation measures to reduce impacts of artificial lighting. Although mitigation schemes such as part-night lighting may help to minimize impacts of nighttime lighting, more tailored schemes for bats should devised to achieve greater conservation impacts.

Table of Contents

List of Tables

List of Figures

List of accompanying material

Author's declaration

The contribution to the chapters in this thesis by the main author, Julie Day (JD) are shown below with contributions indicated from Amy G Fensome (AGF), Cecily E D Goodwin (CEDG), Fiona Mathews (FM), Henry Schofield (HS), James Baker (JBa), Jon Bennie (JBe), Kevin J Gaston (KJG). For additional field assistance, please see acknowledgments.

Chapter 1

Original draft: JD; Review and editing: JD, AGF, FM, KJG.

Chapter 2

Conceptualization: FM, JBe, JD, KJG; Data collection: JBe extracted satellite data and JD compiled the dataset; Statistics: JD; Original draft: JD; Review and editing: CEDG, FM, JD, KJG.

Chapter 3

Conceptualization: FM, HS, JD, KJG; Data collection: JD, JBa; Statistics: JD; Original draft: JD; Review and editing: FM, KJG.

Chapter 4

Conceptualization: JD, KJG; Data collection: JD, JBa; Statistics: JD; Review and editing: FM, HS, JBa, KJG.

Chapter 5

Conceptualization: FM, JD, KJG; Data collection: JD, Statistics: JD; Original draft: JD; Review and editing: FM, JD, KJG.

Chapter 6

Original draft: JD, Review and editing: FM, JD.

Chapter 1: General introduction

Thesis PP 21–41

As the human population grows and civilisation develops, society strives to improve living conditions. These developments often have unintended impacts on the environment. Protecting the environment is of great importance to enable sustainable human population growth, balancing socio-economic issues with environmental concerns. The 2015 world population figure of 7.3 billion is set to increase by 35% to 11.2 billion by 2050 (UN, 2015), and so many policy decisions need to be made about how the needs of people are met within environmental constraints.

1.1 Declines in wildlife

Human actions are putting growing pressure on biodiversity, with global extinction rates 1000 times higher than predicted rates without human activities (Pimm *et al.* 2014). Species richness and abundance in human-dominated landscapes have declined by 13.6% and 10.7% respectively over the last 500 years (Newbold *et al.* 2015) with potentially important consequences for ecosystem function (Loreau *et al.* 2001). Following the recognition that biodiversity provides services to humans, economic assessments have placed values on ecosystem services in the trillions of dollars per year (e.g. Costanza *et al.* 1997). In response, many governments have recognised the value of the environment, putting financial backing to conservation policies (Ferraro & Kiss 2002).

1.2 Urbanisation

Over half of the world's population lives in urban areas (UN, 2015) and with human population expected to increase by a third, urban areas are in turn predicted to triple between 2000 and 2030 (Seto *et al.* 2012). Urbanisation is a broad term which encapsulates many different impacts on the environment including changes to land cover and use, which in turn change biogeochemical processes, hydrological systems, and biodiversity (Grimm *et al*. 2008). One associated feature of urbanisation is the production of pollutants.

1.2 Pollutants

Many human activities produce by-products which can enter the environment unintentionally. These by-products, or pollutants, can have a wide range of effects on the environment, making pollution a key ecological topic for policy (Sutherland *et al.* 2006). Efforts have been made to identify different pollutants and their impacts, however the potential list of agents is vast (Keith & Telliard, 1979). Some of these pollutants are well regulated by specific national and international legalisation. However due to the specificity of these regulations, many pollutants are currently left unregulated. Traditionally the definition of pollution has been restricted to chemicals and materials. For example, the European 2008 ambient air quality directive (2008/50/EC) defines a pollutant as, "any substance present in ambient air and likely to have harmful effects on human health and/or the environment as a whole" but focuses on a set list of chemical compounds: "sulphur dioxide, nitrogen dioxide and oxides of nitrogen, particulate matter (PM10 and PM2,5), lead, benzene and carbon monoxide."

Beyond chemical and material contaminants, pollution can be further expanded to include several less conventional pollutants, such as those produced by wavelengths (e.g. sound and light waves). In these cases, the same principles apply as with conventional types of pollutants in that the pollutant contaminates either air, soil or water and can have direct or indirect impacts on the environment. These types of pollution are not that dissimilar to conventional pollutants.

1.3 Light pollution

1.3.1 Ecological light pollution

Light pollution is a term usually used to describe the obstructing of stars by artificial light and not commonly in the context of the effects of nighttime lighting on wildlife. For instance, the International Dark Sky Association has created several international dark sky reserves whose primary goal is to protect land with quality star viewing, limiting astronomical light pollution (Welch & Dick, 2012). A side aim of these reserves is to preserve the nocturnal environment in general, which may include ecosystems level effects of light pollution. To distinguish astronomical light pollution with the impacts of light pollution on behavioural and population ecology, Longcore & Rich (2004) coined the term “ecological light pollution.”

For a range of organisms, there are many documented physiological and behavioural effects in response to artificial nighttime lighting (Gaston *et al.* 2013, 2014a). A well-known direct impact of artificial lighting is the disorientation of hatchling sea turtles. Sea turtles ordinarily use the visual cue of light reflected on the sea to travel seaward and are confused by lights from beachfront urbanisation

(Salmon & Witherington, 1995) which may cause mortality. In addition to behavioural effects of artificial light, light pollution can also affect physiology. Many biological systems have developed to take cues from natural light patterns such as the length of the day to inform seasonality. For instance, it has long been documented in laboratory studies that light can alter metamorphosis in frogs. The hormone melatonin is key to metamorphosis in frogs and its production is governed by light levels. By disrupting natural light patterns, the speed of metamorphosis is altered (e.g. see Delgado *et al.* 1987).

Physiological and behavioural effects may accumulate and result in demographic effects (Gaston & Bennie, 2014). For example, in response to artificial nighttime lighting, the avian dawn chorus has been documented to start earlier in the day (Arroyo-Solís *et al*. 2013; Dominoni *et al*. 2013), and earlier in the season (Da Silva *et al*. 2015), leading to earlier egg laying (Kempenaers *et al.* 2010). This shift in phenology can lead to mismatches between important life stages and food availability. As the study of the impacts of artificial lighting on wildlife is a relatively new area of study, data exploring population level effects are hard to come by however, there is now evidence of this in insects (Davies *et al.* 2012, 2017).

1.3.2 Light pollution and UK legislation

The Royal Commission on Environmental Pollution was set up in 1970 to advise on environmental issues, and ran until 2011 until governmental spending cuts led to its closure. In growing recognition of concerns for artificial lighting, the Royal Commission on Environmental Pollution published a report on Artificial Light in the

Environment (RCEP, 2009) which highlighted the lack of knowledge of the effects of artificial light on biological systems and the necessity to address nighttime lighting at a national level. In 2016, a petition was put forward to the U.K. government calling for the introduction of legislation on light pollution, highlighting growing public awareness (however the petition was closed without debate or further action). Although there are not laws which specifically mention terms such as ‘light pollution’, there are pieces of U.K. legislation that can be applied to artificial lighting.

Under the Environmental Protection Act 1990, artificial lighting is covered as a potential ‘statutory nuisance’ and so if lighting emitted from a property can be assessed as harmful to human health or a nuisance, action can be sought to remove these light sources. This legislation, however, is limited to light from private properties and is not applicable to street lighting. There are several other pieces of legislation which, although they do not explicitly mention light pollution, can be applicable to the effects of artificial lighting on wildlife. Legislation that protects some species from disturbance includes the Conservation of Habitats and Species Regulations 2010 and the Wildlife and Countryside Act 1981. In addition, the Natural Environment and Rural Communities Act 2006 protects some species requiring an Ecological Assessment for planning purposes and can lead to planning applications being refused.

1.4 Light pollution and bats

Artificial light at night can have impacts on both diurnal and nocturnal organisms and for nocturnal species such as bats, the impacts can be very marked. The effects

include disruptions to circadian rhythms by delaying or halting emergence (Decoursey & Decoursey 1964; Shirley *et al.* 2001; Downs *et al.* 2003; Boldogh *et al.* 2007; Zeale *et al*. 2016), changes to feeding behaviour (e.g. Geggie & Fenton 1985; Rydell & Racey 1995; Lewanzik *et al.* 2014; Avila-Flores & Fenton 2015), modification of predator-prey interactions (Svensson & Rydell, 1998; Minnaar *et al.* 2015; Wakefield *et al*. 2015), alterations to commuting (e.g. Stone *et al*. 2009, 2012) and disruptions to migration (van Gelder 1956; Voigt *et al.* 2017).

In the last ten years, research has emerged showing that street lighting affects species in different ways. For instance, artificial lighting provides foraging opportunities for some insectivorous bat species but can exclude other species from their environment (Table 1.1). Bat species which take advantage of insects around street lights tend to fast-flying and catch their prey in flight (i.e. by aerial hawking) whilst species that are slower flying and glean their prey avoid street lit areas. Although some species of bats may take advantage of insects around street lights, it is unclear whether these short-term foraging opportunities are beneficial overall as there have been no long-term studies and limited research on the impacts on reproduction (see Boldogh *et al.* 2007). It is evident that artificial lighting can still have negative impacts on species that forage around street lights, for example disrupting emergence when lighting is near bat roost entrances (e.g. Downs *et al.* 2003).

Table 0.1 The impacts of artificial lighting on U.K. bat species during foraging and commuting. Sources: [1] Azam *et al*. (2015); [2] Korine & Pinshow (2004); [3] Lacoeuilhe *et al.* (2014); [4] Mathews *et al.* (2015); [5] Russo *et al.* (2017); [6] Rydell (1991); [7] Rydell (1992); [8] Spoelstra *et al.* (2017); [9] Stone *et al.* (2009); [10] Stone *et al.* (2012).

Bat species	Forage or avoid	Evidence
Rhinolophidae		
Rhinolophus hipposideros	Avoid	Absence at lit good quality habitat [2]. Reduced activity on commuting routes outside of maternity roosts following illumination [9,10].
R. ferrumequinum	Avoid	Inferred from *R. hipposideros.*
Vespertilionidae		
Barbastella barbastellus	Forage & avoid	Avoid lit areas for drinking but increased foraging at lights [5].
Eptesicus serotinus	Forage	Positive correlation between light intensity and bat activity [3] however no difference between dark and lit sites in another study [4]. Closely related *Eptesicus nilssonii* forages around streetlights [7] particularly in spring & autumn [6].
Myotis alcathoe	Avoid	Less activity for *Myotis spp.* at lit compared with dark nights in an experimental set up [1] and *Myotis spp.* only observed away from streetlights in an observational study [7]. *Myotis spp.* have fewer bat passes at white and green light compared with dark, however activity not different under red light compared with dark locations [8] and there is a negative correlation between light intensity and bat activity [3]. *M. nattereri* has reduced drinking activity under lights [5].
M. bechsteinii	Avoid	
M. brandtii	Avoid	
M. daubentonii	Avoid	
M. nattereri	Avoid	
M. mystacinus	Avoid	

Nyctalus leisleri	Forage	More activity at lit compared with dark nights in an experimental set up [1] and in an observational study, there was a positive association of activity with lighting and lamp density [4]. In contrast, in other observational studies, there were no significant difference between dark and lit sites recorded [4] and a negative correlation between light intensity and bat activity [3].
N. noctula	Forage	Forages around streetlights [7] with a positive correlation between light intensity and bat activity [3], however in an observation study there was no significant difference between dark and lit sites [4].
Pipistrellus nathusii	Forage	More activity at lit compared with dark nights [1]. *Pipistrellus spp.* have more passes at white and green light compared with dark sites [8].
P. pipistrellus	Forage	Forages around streetlights [7,5], with more activity on lit nights compared with dark nights [1] and at lit sites compared with dark sites [4]. A positive correlation between light intensity and bat activity has been documented [3] and *Pipistrellus spp.* have more passes at white and green light compared with dark sites [8]. In contrast, another study [10] found that a lit treatment night had no short-term effect on activity or feeding compared with dark nights.
P. pygmaeus	Forage	A positive correlation has been documented between light intensity and bat activity [3] however in other studies lit treatment nights had no short-term effect on activity or feeding compared with dark nights [10] and no significant difference has been recorded between dark and lit sites in an observational study [4]. *Pipistrellus spp.* have more passes at white and green light compared with dark sites [8].
Plecotus auritus	Avoid	Only observed away from streetlights [7] and has reduced drinking under lights [5]. *Plecotus spp.* have less activity at lit compared with dark nights in an experimental set up [1]. *Plecotus spp.* show a negative correlation between light intensity and bat activity [3] and fewer bat passes at white and green light compared with dark [8].
P. austriacus	Avoid	Absence in illuminated suitable habitat [2]. *Plecotus spp.* have less activity at lit compared with dark nights in an experimental set up [1]. *Plecotus spp.* show a negative correlation between light intensity and bat activity [3] and fewer bat passes at white and green light compared with dark [8].

1.5 Mitigation of light pollution

All bat roosts are protected under European legislation (Habitats Directive 1992, Annex IV) and for some species, their commuting and foraging areas are also protected (Habitats Directive 1992, Annex II). Currently in some European countries, when lighting presents a potential issue for bats, mitigation is carried out; however, this is usually based on expert opinion rather than systematic peer-reviewed evidence. There are a range of potential avoidance/mitigation options for street lighting that have been proposed: "(i) prevent areas from being artificially lit; (ii) limit the duration of lighting; (iii) reduce the 'trespass' of lighting into areas that are not intended to be lit (including the night sky); (iv) change the intensity of lighting; and (v) change the spectral composition of lighting" (Gaston *et al.* 2012). Many practitioners are faced with the question of which mitigation they should use without much guidance; however, evidence is starting to be collected for bats (Stone *et al*. 2015a).

1.5.1 Keep areas dark

To completely prevent lighting from impacting bats, the areas of the landscape that bats use should be kept totally dark. This is problematic as bats are highly mobile, use large areas, with different parts of the landscape being used for different reasons. This means that dark areas may need to be quite large, such as a designated dark skies reserve. There are several internationally designated dark skies reserves but wildlife reserves are rarely designated based on their light levels (Gaston *et al.* 2015a). Alternatively, key areas of the landscape for bats could be identified and protected. Key areas to keep dark would include areas directly around bat roosts and hibernation sites as lighting in these areas can cause disruptions to circadian rhythms and roost abandonment (e.g. Bolgough *et al.* 2007; Zeale

et al. 2016). Other important areas to keep dark may include commuting routes, foraging grounds, drinking areas and swarming sites. These areas are hard to identify without detailed studies of individual roosts from radio-tracking studies, however by identifying key habitat features, it may be possible to predict where high levels of bat activity are likely to be and how developments may interfere with these. For instance, a theoretical study has attempted to model bat movements using circuit theory, predicting bat movements from roosts to foraging sites, setting landscape features that facilitate movements such as hedgerows as low resistance and features that restrict movements such as street lights and buildings as high resistance (Bennie *et al.* 2014b). This model has not been compared against actual bat activity, however if tested, these techniques may enable effective management on landscape scales, highlighting areas that would be highly beneficial to remain dark. Refinement is needed to understand how different habitat characteristics predict bat activity and how street lighting alters this relationship.

1.5.2 Limit the duration of lighting

Another suggestion is to limit the duration of lighting, reducing light pollution temporally rather than spatially. This could be implemented with a Central Management System (CMS), timers or sensors (Stone *et al*. 2015a) to use lighting only when people are active on the streets. Following the 2008 financial crises in the U.K., many local authorities started to implement part-night lighting, limiting the duration of lighting at night (typically switching lights off between midnight at 5am) to save money on their street lighting electricity expenditure. This has allowed observational studies to monitor the effects of part-night lighting as a mitigation technique (see Azam *et al*. 2015). These part-night lighting regimes

are designed with human activity in mind rather than wildlife activity so further work could to explore part-night lighting regimes based around wildlife activity patterns.

1.5.3 Reduce the trespass of lighting

Often lighting schemes illuminate areas outside of those intended. Lights can be fitted with shields to reduce this light spill or replaced with more modern light-emitting diode (LED) lighting that can be directed more effectively. In an artificial set up of LED street lighting, *R. hipposideros* activity was reduced on the side of the hedge where lights were set up, however there was no effect on bat activity on the unlit side of the hedge (Stone *et al*. 2012). This demonstrates that it may be possible to limit the effects of street lighting through careful placement and choice of street lights. One concern with LED lighting, however, is that it creates a more uniform illumination across the street compared with more traditional lights. In an observation study of *P. pipistrellus*, Hale *et al*. (2015) found that bats were more likely to cross roads at darker gaps between street lights, which may not be present with LEDs. An additional concern for light trespass is sky glow (caused by upwards light trespass), which can illuminate unintended areas tens of kilometres from the light source (Kyba *et al.* 2011), however this is very understudied.

1.5.4 Change the intensity of lighting

A popular question for lighting engineers and ecological consultants is: what is the maximum intensity that can be used to prevent impacts of lighting on bats? Unfortunately, there does not seem to be an easy answer for this. Natural nighttime light levels are very low, with the brightest full moon on a clear night around 3 lux. In many bat species, on nights with bright moon conditions, activity is reduced which is known as the phenomenon

of lunar phobia (see Kronfeld-Schor *et al.* 2013 for a review). This would suggest that it would be necessary for artificial light levels to be below 3 lux to have no impact on bat activity. This can be seen in *R. hipposideros* and *Myotis spp.* where low artificial light levels of 3.6 lux significantly reduced commuting activity out of roosts compared with dark nights (Stone *et al.* 2012). This is the only study experimentally manipulating light intensities on commuting routes and so thresholds of light intensity have not been identified for any species that can be used for management. Such low light levels as seen in Stone *et al.* (2012) are unlikely to provide much benefit for human use. An additional concern with reducing light intensities is that this is often done by reducing the pulse rate of light, which to humans is perceived as a low intensity but to other organisms is perceived as light flickering (Inger *et al.* 2014) which has unexplored additional impacts.

1.5.5 Change the spectrum of lighting

Organisms differ in how they perceive light, not only by intensity but also by light spectrum. Depending on the receptors an organism has, the organism will sense different wavelengths of light (Figure 1.1 A). Different street light technologies produce different light profiles (Figure 1.1 B) and so some street lights will be perceived more than others to some organisms.

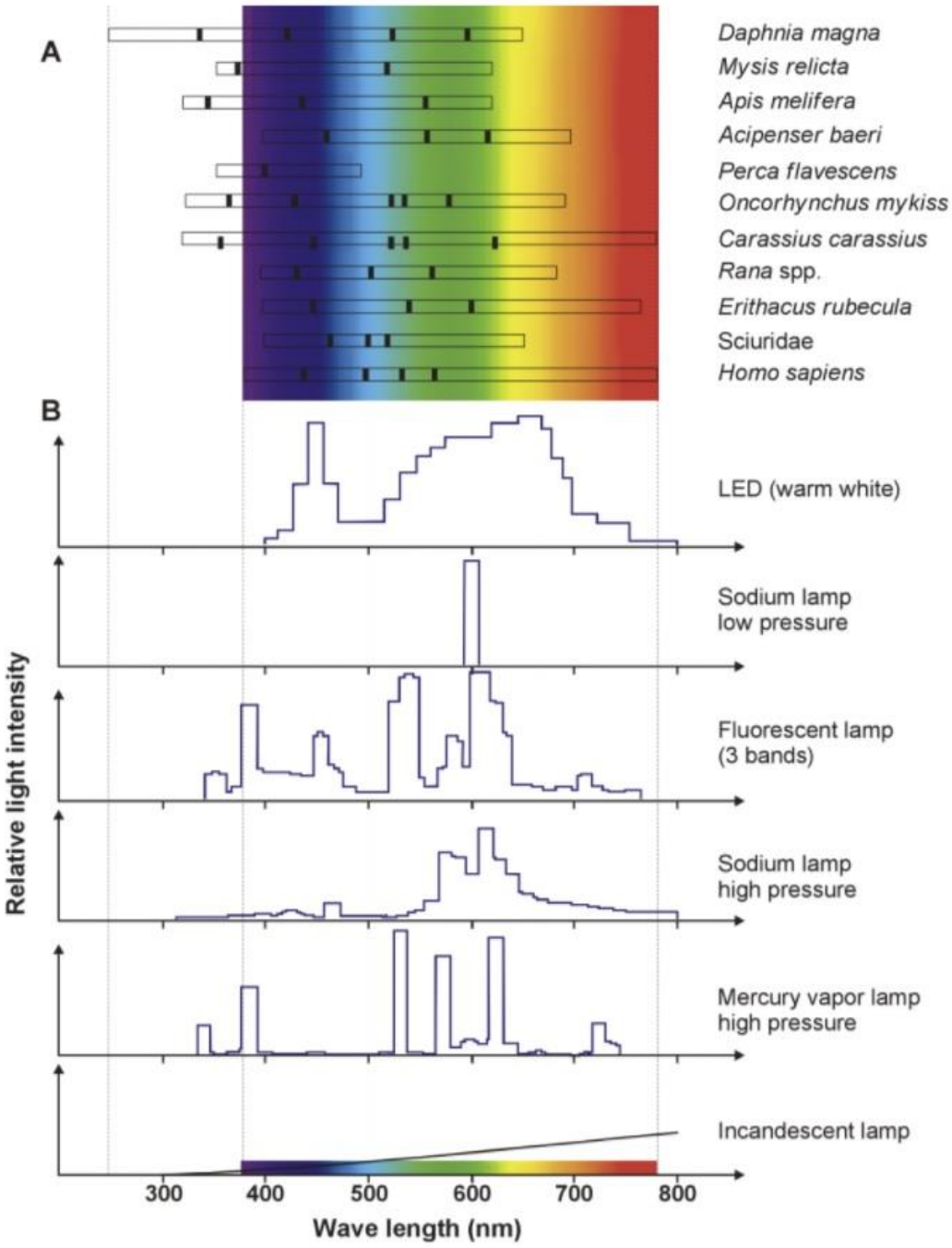


Figure 1.1 A) Wavelength sensitivities in a range of organisms. Open rectangles represent the total breadth of wavelengths which are visible for each organism and black rectangles indicate peak sensitivity for different colour receptors within each organism. B) Light profiles of commonly used street lights. Taken from Perkin *et al.* (2011).

For insectivorous bats, there are two factors to consider when exploring which spectrum of light is likely to impact on them. One is how the bat itself perceives the light and the other is how its prey perceives light. Many insects are attracted to short wavelengths (e.g. see Somers-Yeates 2013; van Langevelde *et* al. 2011) and so for bats that foraging around street lights, lights which emit these wavelengths may provide foraging opportunities and increase bat activity. This has been documented for *E. nilssonii,* (Rydell 1992), *P. pipistrellus* (Lewanzik & Voigt 2016; Spoelstra *et al.* 2017; Stone *et al*. 2015b) and *P. pygmaeus* (Stone *et al*. 2015b). Ultraviolet (UV) light levels seem to very important in determining if foraging bats are attracted to street lit areas, as in a switch from low pressure sodium lamps to LED (both lacking UV), there was no detected difference in bat activity for *P. pipistrellus*, *P. pygmaeus* and *Nyctalus* spp. (Rowse *et al*. 2016).

For bats that avoid street lit areas all together, wavelengths which they cannot perceive may provide a good alternative to conventional street lamps where lighting is necessary for humans. *Myotis* spp. appear to be sensitive to short wavelengths, as seen in a switch from mercury vapour lamps (with short wavelengths present) to LED lamps where activity increased (Lewanzik & Voigt 2016). *Myotis* spp., *Plecotus* spp. and *P. pygmaeus* do not appear to be affected by red light (see Spoelstra *et al.* (2017) for *Myotis* spp. and *Plecotus* spp. and Downs *et al.* (2003) for *P. pygmaeus*).

1.6 Thesis aims

With the rapid expansion of urban areas and advancing technologies in lighting, there is a great need from conservation practitioners for scientific studies and practical advice. There are still many gaps in knowledge on firstly how street lighting affects bats but also

what mitigation is effective. The aim of this thesis was to answer how street light affects bats on a landscape scale, how habitat characteristics interact with these effects and explore potential mitigation schemes. Several U.K. bat species were studied, however *R. ferrumequinum* was investigated in more depth due to the high conservation status of this species and lack of data on how street light affects its behaviour. There are many knowledge gaps around the mitigation of light pollution on bats and so this thesis explored part-night lighting.

1.6.1 An overview of the exposure of U.K. bat species to light pollution

In Chapter 2 I set out to assess the national exposure of bat species to artificial light at night. I explore the current and past levels of artificial lighting around bat roosts, to reveal the extent of artificial light at night at sensitive areas around maternity roosts. At localised points around individual street lights, artificial light at night alters bat behaviour (Table 1.1). I investigated whether these local responses are reflected in landscape level effects. I asked if light levels around bat roosts are different to those 'available' to them, with the hypothesis that light levels in landscapes around bat roosts are darker than light levels in 'available' areas. Bat species with different wing morphology and feeding behaviours respond to artificial lighting in different ways with some taking advantage of insects around street lights (Table 1.1) and so I explored whether these differences in species can also be seen in light levels around their roosts. I expected that bat species which take advantage of insects around street lights have higher levels of light in the landscapes around roosts than species that avoid street lights.

To date there has been no empirical evidence to show if short-term behavioural effects of artificial lighting on bat activity lead to long-term population effects. In Chapter 2 I ask if light levels in the landscapes around bat roosts affect roost count with the hypothesis that larger roosts will have lower light levels than smaller roosts. I also ask if, as globally the amount of artificial light is increasing, light levels around bat roosts have changed over time, expecting to find that they have increased over time.

1.6.2 The impacts of artificial lighting on the *R. ferrumequinum*

There are knowledge gaps for species that are rare and hard to study. For example, *R. ferrumequinum* has no published data on behavioural responses to artificial lighting, however a closely related species, *R. hipposideros* has reduced commuting activity on hedgerows outside of maternity roosts when lit with artificial lighting (Stone *et al* 2009, 2012). In Chapter 2, mean light levels in the landscapes around maternity roosts for *R. ferrumequinum* were lower than those for species which take advantage of insects around street light, however these results were not significant, which may be due to the low sample size in the National Bat Monitoring Programme for this species. In Chapter 3 I ask if like *R. hipposideros*, *R. ferrumequinum* also exhibits light avoiding behaviour and if these behaviours are still present when street lights are permanent fixtures rather than temporary lights (as in Stone *et al*. (2009, 2012)). I explore this in detail with a high density of bat sampling points at a landscape scale to gather detailed information on this rare and hard to study species. I expected to find that there would be more bat activity at dark locations compared with permanently street lit locations.

In Chapter 3, I utilised the large dataset collected to explore some potential mitigation questions. Firstly, I explored the potential effectiveness of using lights with different light spectra and intensities. Some bat species appear to be less affected by lights with long wavelengths (e.g. red light) than shorter wavelengths (e.g. ultra violet and blue light) and so I expected shorter wavelengths to have a greater negative effect on *R. ferrumequinum* activity than longer wavelengths. In addition, I also expected for bat activity to decrease as intensity of light increased for all light spectra. Secondly, I examined the potential merits of guidance for street light placement (avoiding placing street lights at sensitive areas). As bats are highly mobile, some habitat features are more important than others and so these areas may be more sensitive to artificial lights than other areas. I expected to find that at favourable habitat locations, street lit locations would have lower bat activity than unlit locations whilst at unfavourable habitat locations, for street lighting to have no effect on bat activity.

1.6.3 Part-night lighting- in theory

Following the findings in Chapters 1–3 that artificial light at night can have negative impacts on bats, I focused my remaining analyses in Chapters 4–5 on examining part-night lighting, a potential mitigation option that could be implemented on a large scale to existing and future street lights. In Chapter 4, using a subset of the *R. ferrumequinum* dataset collected in Chapter 3 from only dark locations, I explored activity patterns of *R. ferrumequinum* throughout the night. This was done to explore the potential benefits of part-night lighting, answering when most bats are active and how this conflicts with the human needs for lighting (when people are most active on the streets). I expected to find that there would greater activity soon after sunset and before sunrise compared with other parts of the

night. As part-night lighting schemes often operate after midnight, I expected that the majority of bat activity would not be captured by proposed part night lighting schemes. This was the first piece of research published investigating the impacts of part-night lighting on bats as a potential mitigation option.

1.6.4 Part-night lighting- in practice

In Chapter 5, I then tested the theories set out in Chapter 4 with a before and after study of part-night lighting. This study was not targeted at any specific species and examined the impacts of part-night lighting on the species assemblages found in towns in Devon. I questioned whether switching off street lights between 1am and 2am changes the levels of bat activity compared with full night lighting. I expected to find that for species that take advantage of insects around street lights for there to be less activity when the lights were switched off compared with when they were switched on due to loss of foraging opportunities. For bat species that do not take advantage of insects around street lights and avoid street lit areas, I expected to find more bat activity when the street lights were switched off compared to when they were on. A combination of the analysis in Chapter 4 and 5 were intended to give empirical evidence for the effectiveness of a proposed lighting scheme (part-night lighting) to reduce the impact of artificial lighting on wildlife.

Chapter 2: The impacts of lighting on bat roost location and colony size

Thesis PP 43–64

2.1 Summary

Artificial night at light is increasingly becoming recognised as a harmful pollutant for many organisms and is associated with increased human population density and urbanisation. Bats have been shown to be sensitive to artificial lighting during both foraging and commuting. Here we assess the impacts of nighttime lighting on bat roost location and colony size. We employ newly developed techniques using satellite imagery of artificial nighttime lights and pair these with long-term data for seven bat species in the Britain (*Eptesicus serotinus*, *Myotis nattereri*, *Pipistrellus pipistrellus*, *P. pygmaeus*, *Plecotus auritus*, *Rhinolophus hipposideros* and *R. ferrumequinum*). We compared bat roost light levels with those of random locations in the landscape. Differences in roost light levels between species were examined. We also looked at roost size in relation to nighttime light levels and analysed the change in light levels over time. *P. pipistrellus*, *P. pygmaeus* and *P. auritus* had significantly higher light levels around roosts than random locations within their distributions. When comparing light levels between bat species, *P. pipistrellus* and *P. pygmaeus* had significantly higher light levels than *R. hipposideros, M. nattereri* and *P. auritus. E. serotinus* had significantly higher light levels than *R. hipposideros* and *M. nattereri*. Within all species, roost size was significantly negatively correlated spatially with light levels, however most of the monitored bat roosts were not located in sites where light levels have increased appreciably over time. Globally, urban areas are expanding at twice the rate of their populations, increasing the probability that street-lighting will encroach further into dark areas. Artificial light at night will likely restrict population sizes of bat roosts and may impact on the resilience and persistence of those roosts.

2.2 Introduction

With over half of the world's human population now living in cities and towns (UN, 2015), increasing attention has been given to the impacts of urbanisation on the environment (e.g. Alberti, 2005; Gaston, 2010; Seto *et al*., 2012). One of the characteristics of urbanisation is increased artificial nighttime lighting (from a diversity of sources, including street lighting, advertising lighting, architectural lighting, security lighting, domestic lighting and vehicle lighting). This has been highlighted in recent years as a significant environmental concern (Rich & Longcore, 2006; Hölker *et al*., 2010b; Gaston *et al*., 2013, 2015a). There have been many documented physiological and behavioural responses to artificial nighttime lighting by a range of organisms (Gaston *et al.* 2013, 2014a). With artificial lighting estimated to be increasing at a rate of 6% per year globally (Hölker *et al*., 2010a), it is imperative to understand its ecological consequences.

One long-lived group of organisms at risk from artificial nighttime lighting is bats. Some species are particularly sensitive to artificial nighttime lighting, with documented disruptions to circadian rhythms (Laidlaw & Fenton, 1971; Downs *et al.*, 2003; Boldogh *et al*., 2007; Zeale *et al*., 2016), foraging (Rydell, 1992; Lewanzik & Voigt, 2014) and commuting (Stone *et al.,* 2009, 2012; Threlfall *et al*., 2013). For other species, artificial light at night may have foraging benefits through the congregations of invertebrates at street lights (Rydell, 1992; Lacoeuilhe *et al*., 2014). Such behavioural impacts may affect abundances and distributions, leading to changes in species community composition (Arlettaz *et al*., 2000).

Whilst several studies have demonstrated that lighting has impacts on foraging and commuting activity of bats, it is unclear what the full extent of artificial lighting is around bat

roosts and whether individual points of illumination disrupt whole landscapes. As bats are highly mobile it is important to study the impacts of artificial lighting at large spatial scales. In the last decade, there has been an increase in the use of satellite imagery to derive information on artificial nighttime light at large scales and to pair this with biological data (e.g. Dwyer *et al.*, 2013; Kamrowski *et al.*, 2014). This has relied heavily on the nighttime lights dataset from the National Geophysical Data Center's (NOAA) Defense Meteorological Satellite Program (DMSP) operational linescan system (OLS). While this provides the only long time-series of such data, the lack of formal cross-calibration of the different sensors that have been used at different times has previously prevented direct comparisons over the years (Elvidge *et al.*, 2001). There are, however, now methods available to overcome these issues (Bennie *et al*., 2014a).

Here we present a large scale, long-term study on artificial nighttime light and bat roosts. Historic data on artificial nighttime lighting were derived from satellite images, using recently developed techniques to permit information from different satellites to be combined (Bennie *et al*., 2014a). These data were combined with long-term data on bat roost locations and sizes from the National Bat Monitoring Programme. To test whether local effects of artificial light on commuting and foraging have landscape level effects, we assessed light levels around bat roosts and randomly generated locations. We hypothesise that the landscapes around bat roosts will be darker than light levels at randomly generated locations. As some bat species take advantage of insects around street lights whilst others avoid lit, we compared light levels around bat roosts between species with the hypothesis that bat species that take advantage of insects around street lights for foraging have higher levels of light than species that avoid street lights all together. We then examined if light levels affect

roost count with the hypothesis that larger roosts have lower light levels in the landscapes around roosts compared with smaller roosts. Finally, as globally light levels are increasing, we explored if this is trend is reflected in the light levels around bat roosts, expecting that light levels have increased over time around bat roosts.

2.3 Materials and Methods

2.3.1 Colony counts

Data on bat roost locations and colony size were taken from the Bat Conservation Trust National Bat Monitoring Programme (NBMP). Maternity roosts were monitored longitudinally by volunteers from 1997–2012. Volunteers selected sites for monitoring and carried out emergence counts. For most species, emergence counts were taken between 6th-25th June, except for *R. hipposideros* and *R. ferrumequinum* for which they were conducted between 29th May- 27th June and 7th-21st July respectively. These timings ensured that counts were made before young were flying. At sunset, bats were counted as they emerged from roosts, taking note if any bats re-enter the roost to avoid double counting bats. Seven species were included in the current analysis (Figure 2.1): lesser horseshoe bat (*Rhinolophus hipposideros*), greater horseshoe bat (*R. ferrumequinum*), Natterer's bat (*Myotis nattereri*), common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*P. pygmaeus*), Brown long-eared bat (*Plecotus auritus*) and serotine bat (*Eptesicus serotinus*). Horseshoe bats (*Rhinolophus spp.*) and serotine (*E. serotinus*) have restricted geographical distributions unlike the other species. Roosts were included in the analysis if there were at least 3 years of counts during the study period.

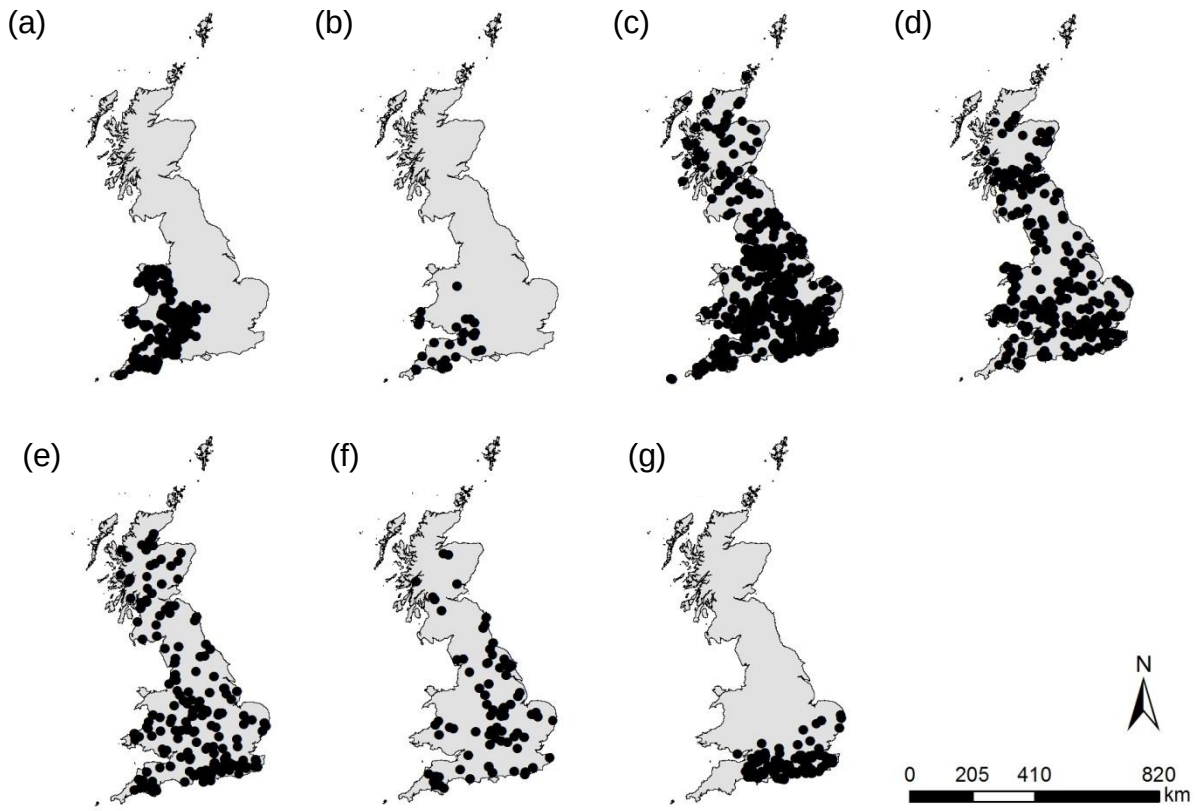


Figure 2.1 Distribution of National Bat Monitoring Programme roosts: (a) *R. hipposideros*, (b) *R. ferrumequinum*, (c) *P. pipistrellus*, (d) *P. pygmaeus*, (e) *P. auritus*, (f) *M. nattereri* and (g) *E. serotinus*.

For each year, two emergence counts were made during specific time windows, which were designed to be prior to the emergence of volant young (see Appendix 2.1). Where multiple counts were made within a year, the maximum roost count value was taken to allow for late arrival of females to the maternity colonies.

To consider regional variation between roosts from factors such as climatic conditions and habitat characteristics (e.g. woodland density), each roost was assigned a civil

administration code for region (see Appendix Figure 2.1 for a list of the regions and boundaries).

2.3.2 Artificial nighttime lighting data

Nighttime light levels were extracted from stable cloud free satellite images from the Defense Meteorological Satellite Program (DMSP) Operational Linescan System (OLS), (freely available from the National Geophysical Data Center, USA). This is available from 1992–2012 at a resolution of 3 km divided into 500m raster squares. A full dataset of 12 years was extracted to match the years of bat data. Data were calibrated to compensate for differences in satellites and shifts in location (see Bennie *et al*., 2014a for methods). For comparative purposes, data at a higher resolution of 300m were also extracted from the Suomi National Polar-Orbiting Partnership (NPP) satellite (National Geophysical Data Center, USA). Data were only available in this dataset from 2012 and were compared with the 2012 subset of the DMSP-OLS data.

Each roost location was buffered by the sustenance zone (an area where most bat activity is concentrated, and hence the area considered of most conservation value) and maximum home range area (the maximum distance a bat will travel from its maternity roost). These values were derived from a review of distances travelled from roosts in the literature (Table 2.1). Mean light exposures within these buffers were calculated, and where pixels crossed the buffer boundary, the values were weighted according to the percentage that each pixel fell within the buffer area.

Table 2.1 Maximum home-range distance and sustenance zone derived from radio-tracking studies.

Species	Maximum home-range radii (km)	Sustenance zone (km)	References
R. hipposideros	5	2	(Holzhaider *et al.* 2002; Motte & Libois 2002; Bontadina *et al.* 2002; Reiter *et al.* 2012)
R. ferrumequinum	12	4	(Ransome & Hutson 2000; Billington 2002, 2003; Bontadina 2002; Bontadina *et al.* 2002; Dietz *et al.* 2013)
M. nattereri	6	1	(Smith 2000; Lundy et al. 2012)
P. auritus	3	1.5	(Entwistle, Racey & Speakman 1996; Ashrafi *et al*. 2013)
P. pipistrellus	4	1.5	(Nicholls & Racey 2006; Davidson-Watts *et al.* 2006)
P. pygmaeus	3	2	(Nicholls & Racey 2006; Davidson-Watts *et al.* 2006; Stone *et al.* 2015b)
E. serotinus	7	2	(Catto *et al.* 1996; Robinson & Stebbings 1997)

2.3.3 Random locations

To assess whether the light levels around bat roosts differed from the surrounding landscape, random locations were generated in ArcMap 10 (ESRI Inc. 2006). For each species, 1000 random locations were generated within the species' distribution, taken from IUCN range maps (IUCN 2008a, 2008b, 2008c, 2008d, 2008e, 2008f, 2008g). Around

these random locations, light levels were extracted at roost sustenance and home range distances as was done for bat roosts.

2.3.4 Statistical analysis

2.3.4.1 Comparison of light exposure at roosts and random locations

Light levels at roosts were compared with those available in the landscapes within each species' range using linear modelling (LM) with a Gaussian error structure the residuals were homogenous and normally distributed. For each model, the light profile around roosts was fitted as the response variable with a two-level fixed effect specifying whether the location was a bat roost or a randomly generated location (actual roost factor). The bat species and the actual roost factor were specified as fixed factors, and the interaction of these two terms was tested. Where only one year of data was used (for both the Suomi-NPP and DMSP-OLS datasets), linear models were run, using the mean light values in the home range, and another LM using the mean light values from the sustenance zone. Analyses were then conducted using the entire available data for 1997-2012 (based on DMPS-OLS only) with linear mixed models, with random effects were specified for site and year, one model using home range values and another using sustenance zone values. These six models were then repeated using data subsets for each of the seven species, removing the fixed effect of species.

2.3.4.2 Species differences in light exposure

To compare the levels of light exposure around the roosts of different species, generalized linear mixed models (GLMMs) were run with Gaussian error distributions as the residuals were homogenous and normally distributed. The light profile around roosts was

fitted as the response variable, with a random effect for region (11-level factor) (to consider the differences in distributions between species) and random effects for site and year in the models using the full DMSP-OLS dataset. Species was fitted as a fixed effect. Tukey's *post-hoc* tests were run on all models to determine significance levels between species.

2.3.4.3 Effect of light exposure on roost count

To test the effect of light level on roost size, roost count was fitted as a response variable with light level in the landscape and species fitted as fixed effects. For the two models using the full DMSP-OLS datasets, random effects were fitted for site, year and region. For the remaining four models where only one year of data was used, only region was fitted as a random effect. Negative binomial error structures were used, as this produced the best fitting models (compensating for over dispersion and producing lower AIC values) in comparison to those with a Poisson error structure.

2.3.4.4 Change in light profile over time

Changes in light profiles were assessed in models with light level specified as the outcome variable and year (continuous), region and species designated as fixed effects. Roost location was specified as a random effect to account for the repeated measurements over time. An interaction was fitted between year and species to determine whether there were differences in the change in light exposure around roosts between species. An additional interaction was fitted between year and region to assess if regions experienced different changes in light levels over years. GLMMs were run with Gaussian error distributions as the residuals were homogenous and normally distributed.

2.3.4.5 Statistical program and packages

All analyses were carried out using R (v.3.0.3). GLMMs and LMs were fitted using the package lme4 (v.1.1-7). *Post-hoc* Tukey's tests were performed with multcomp (v.1.3-3) for comparisons between species and phia (v.0.2-0) to test for significant levels within interactions. For GLMMs, marginal and conditional R^2 values (R^2_m and R^2_c respectively, Nakagawa & Schielzeth, 2013) were calculated using the package MuMIn (v.1.9.13). Overall significance levels were calculated using ANOVAs with lmerTest (v. 2.0-20).

2.4 Results

A total of 1,690 unique roosts were included in the analysis with DMSP-OLS data and 719 with Suomi-NPP data (see Appendix Table 2.1 for the number of roosts per species). For ease of interpretation, results are presented using the DMSP-OLS values extracted from roost sustenance distances with further information on additional datasets and models given in the Appendix.

2.4.1 Comparison of light exposure at roosts and the wider landscape

The mean light values were higher at bat roosts compared with random locations for all species (Figure 2.2) although not all of these differences were statistically significant. The differences between the light profiles at bat roosts and random locations varied significantly between species ($F_{6,8674.4} = 9.00$, $p<0.001$, $R^2_{GLMM(M)} = 0.05$, $R^2_{GLMM(C)} = 0.99$). In the species-specific models, light profiles were significantly lower at random locations compared to actual roosts for all values for *P. pipistrellus, P. pygmaeus* and *P. auritus.* For all other species, there was no significant difference (Table 2.2).

In all models using DMSP-OLS or Suomi-NPP in roost sustenance and home range areas, there was a significant difference between light exposure around bat roosts and random locations across species (Appendix Table 2.2.). In the species-specific models, the difference in light exposure between bat roosts and random locations was significant for *P. pipistrellus* and *P. pygmaeus* across all datasets, however for *P. auritus* the differences were only significant using the DMSP-OLS datasets and not the Suomi-NPP datasets (Appendix Table 2.2).

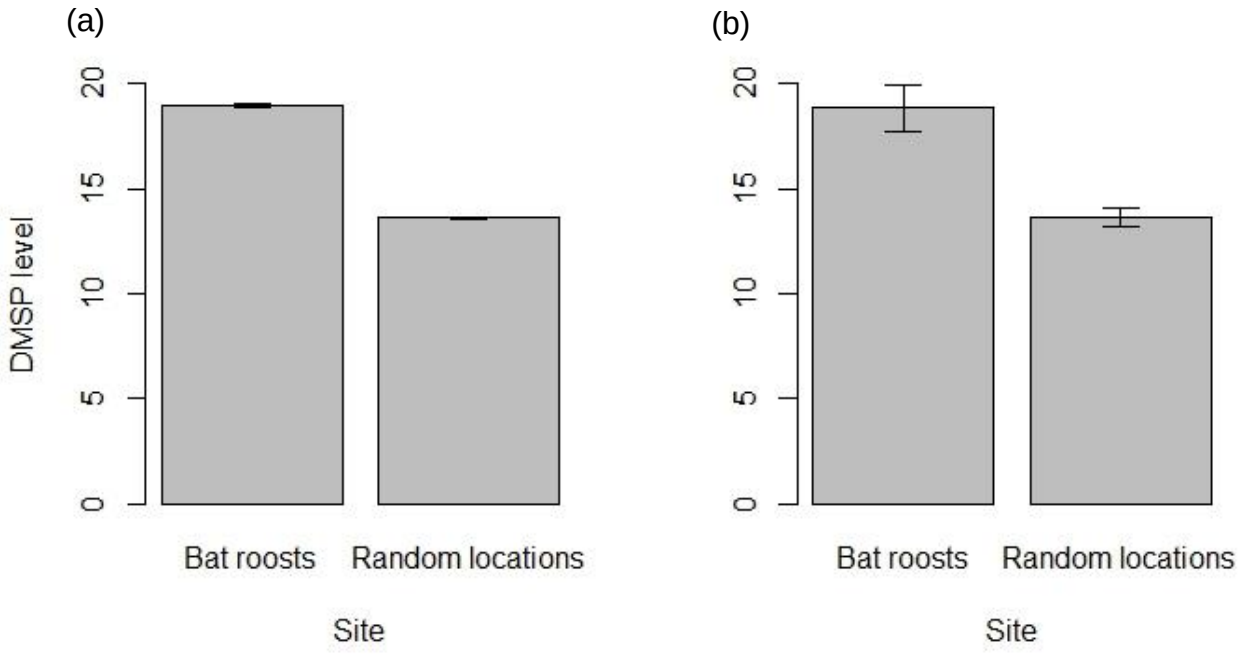


Figure 2.2 Mean (± standard error, SE) Defense Meteorological Satellite Program Operational Linescan System satellite light levels in the roost sustenance zone for bat roosts and random locations from (a) the raw data and (b) model predictions accounting for variation across sites, years and species.

Table 2.2 Model outputs comparing random locations with roost light profiles for species-specific models. F = F-value, df = degrees of freedom, p = *p*-value where *p*<0.05 *, *p*<0.01 ** and *p*<0.001 ***, $R^2_{GLMM(M)}$ = marginal R^2, $R^2_{GLMM(C)}$ = conditional R^2 and estimate = slope estimate.

Species	F	df	p	$R^2_{GLMM(M)}$	$R^2_{GLMM(C)}$	estimate
E. serotinus	3.06	1, 1131	0.08	0.003	0.991	-2.69
M. nattereri	0.06	1, 1088	0.81	6.4E-05	0.99	-0.44
P. pipistrellus	79.65	1,1542.2	***	0.052	0.99063	-8.58
P. pygmaeus	60.25	1, 1399.1	***	0.045	0.99065	-7.96
P. auritus	9.34	1, 1195	**	0.009	0.98983	-3.81
R. ferrumequinum	1.73	1, 1027.9	0.19	0.002	0.99253	-2.97
R. hipposideros	1.27	1, 1293.1	0.26	0.00111	0.98733	-0.89

2.4.2 Species differences in light exposure

There were significant differences between species in their light exposure around roosts ($F_{6,\ 1683.9} = 16.96$, $p<0.001$, $R^2_{GLMM(M)} = 0.056$, $R^2_{GLMM(C)} = 0.988$). The species that typically opportunistically forage around street lights (Table 1.1) had higher mean light levels than species that always avoid lit areas (Figure 2.3). *R. hipposideros, M. nattereri* and *P. auritus* all had significantly lower light levels than *P. pipistrellus* and *P. pygmaeus*. *R. hipposideros* and *M. nattereri* also had significantly lower light levels than *E. serotinus*. There were no significant differences between *R. ferrumequinum* and any other species.

There were significant differences between species light profiles around roosts for all models used. There were more significantly different pairs of species using the DMSP-OLS datasets compared with the Suomi-NPP datasets (Appendix Table 2.3).

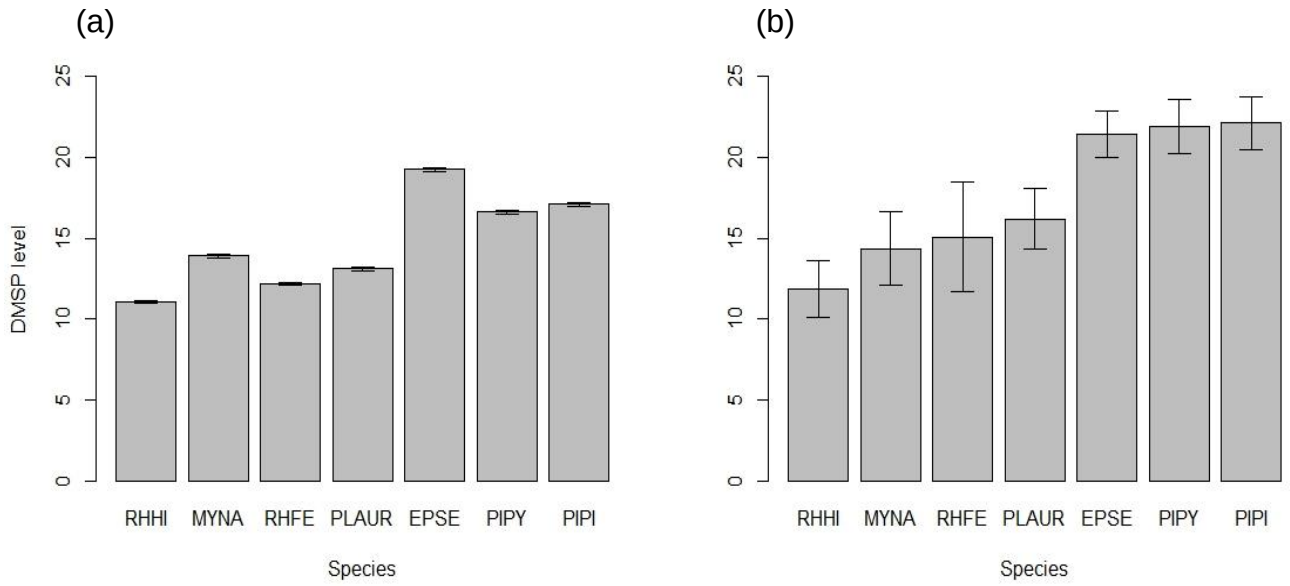


Figure 2.3 Mean (± SE) Defense Meteorological Satellite Program Operational Linescan System satellite light levels in the roost sustenance zone for bat roosts by species from (a) the raw data and (b) model predictions accounting for variation across sites, years and species. Species codes: *R. hipposideros* (RHHI), *M. nattereri* (MYNA), *R. ferrumequinum* (RHFE), *P. auritus* (PLAUR), *E. serotinus* (EPSE), *P. pygmaeus* (PIPY), *P. pipistrellus* (PIPI).

2.4.3 Effect of light exposure on roost count

There was a significant negative effect of light level on roost count (χ^2 = 583.51, d.f. = 6, p<0.001) and roost count differed significantly between species (χ^2 = 56.56, d.f. = 1, p<0.001) (Figure 2.4). Both species and light level had a significant effect on roost size using all datasets (Appendix Table 2.4). For all datasets, as light levels increased, predicted roost size decreased.

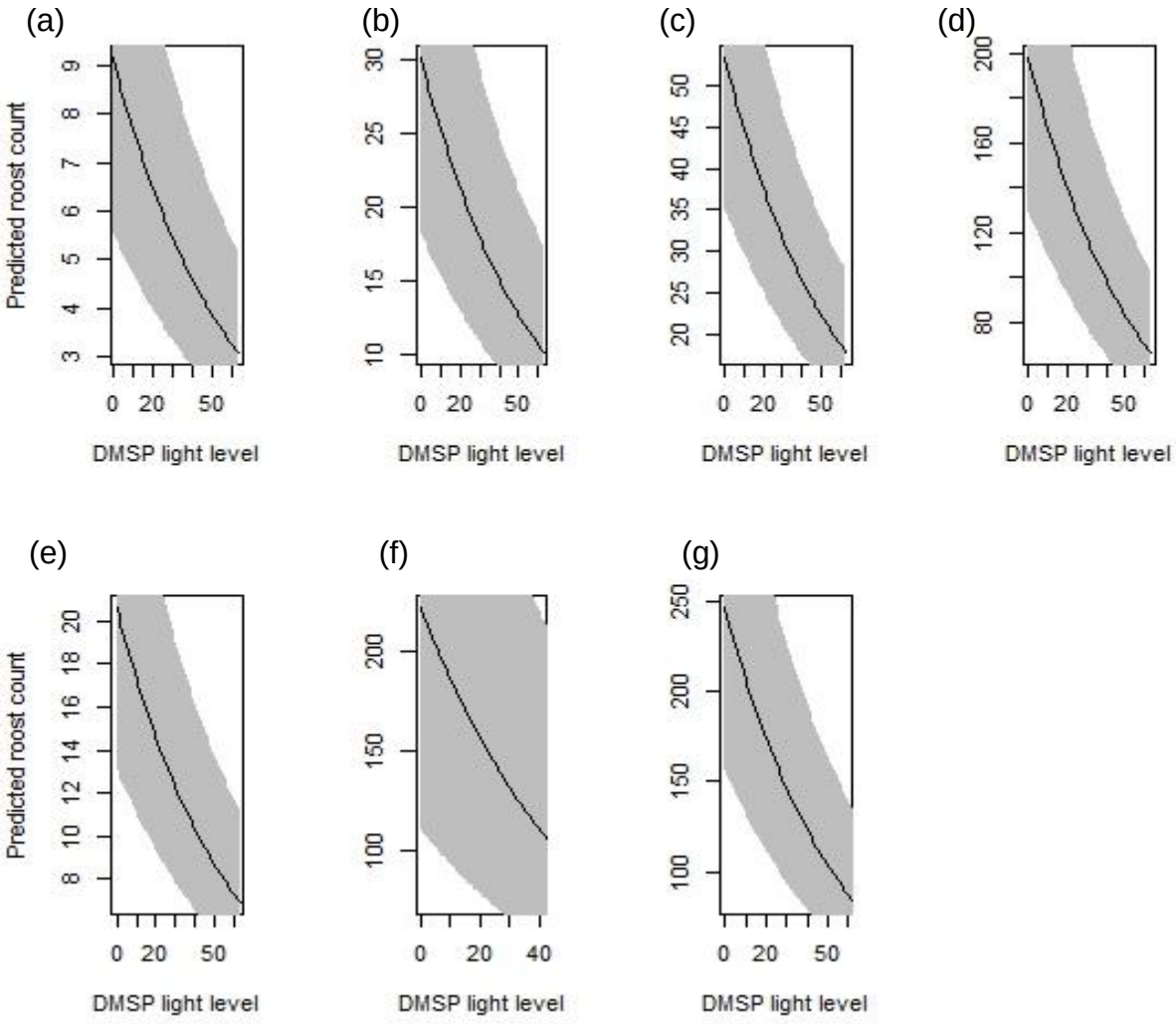


Figure 2.4 Predicted population size at varying light exposure level (Defense Meteorological Satellite Program Operational Linescan System satellite light levels) by species. Solid black line gives the predicted values and grey shading shows the confidence intervals. (a) *E. serotinus*, (b) *M. nattereri*, (c) *P. pipistrellus*, (d) *P. pygmaeus*, (e) *P. auritus*, (f) *R. ferrumequinum*, (g) *R. hipposideros*.

2.4.4 Change in light levels over years

The change in light levels over years differed significantly between species ($F_{6, 33801}$ = 5.358, p<0.001) and region ($F_{10,33827}$ = 44.486, p<0.001), however all differences detected in light levels were of a small magnitude (<0.1 DMSP-OLS unit/year) and therefore are unlikely to represent true changes in light levels. Year, species and region accounted for small levels of the variation in the light readings ($R^2_{GLMM(M)}$ = 0.06, $R^2_{GLMM(C)}$ = 0.99). Estimates for changes in light levels over years for species and years are found in (Appendix Table 2.5).

2.5 Discussion

Globally, many bat species have poor conservation status due to a variety of anthropogenic pressures (Mickleburgh *et al*., 2002). Although bats are sensitive to artificial light pollution (Mathews *et al*., 2015; Stone *et al*., 2015a), the landscape around their roosts are often not protected from nighttime lighting. With artificial nighttime light levels likely to continue to increase with human development (Cinzano *et al*. 2001), areas around many bat roosts may be exposed to higher levels of light pollution in the future.

To date most research on the effects of artificial nighttime lighting on bats has been on behavioural changes at point locations. A reduction in foraging and commuting activity can increase energy expenditure, and so it is often assumed will have an overall negative effect on fitness. Here we show that larger roosts are found in darker landscapes, which may reveal a preference for bats to roost in landscapes that have low light levels and that high light levels restrict bat population sizes. The results presented here, show the effect of nighttime lighting in isolation however artificial lighting is associated with human

infrastructure and developments, and is scarcer in more remote areas with higher covered of natural habitats. It is difficult to disentangle these factors at the broad landscape scales of interest here, however, the results documented here are consistent with the known behavioural effects.

To determine if bats discriminated against lit landscapes, we compared the levels of artificial lighting at randomly generated locations with those at bat roosts. There was no evidence for such discrimination. Indeed, for three species (*P. pipistrellus, P. pygmaeus* and *P. auritus*) roosts had significantly higher levels of light in the surrounding landscapes than the random locations. This may suggest that these species select lit landscapes whilst the others do not. However, there are other explanations. Other landscape requirements may take precedence over light levels leading to roosts being in lighter landscapes than those available to them. In a habitat suitability study for *P. austriacus* at a scale of 1 km surrounding bat presence records, weather variables were found to be large contributors to habitat suitability models and so light variables were discarded (Razgour *et al.*, 2011). In addition, woodland cover has been shown to be a large predictor of roost location of UK bat species (Boughey *et al.* 2011). Our findings here may be due to the nature of the NBMP in that roosts included in the monitoring program are biased towards buildings and manmade structures where they can easily be identified by volunteers (Barlow, *et al*. 2015) and the randomly generated locations were not constrained in this way. The preference for some species to roost in buildings may have led to many roosts being in light landscapes. These roosts are likely to be suboptimal locations and have restricted population sizes due to the high light levels. This would be consistent with our finding for larger roosts to be found in darker landscapes. In a smaller-scale study, analysing *R. ferrumequinum* population trends

from the NBMP dataset, Froidevaux *et al.* (2017) found artificial light at night has an overall negative effect on colony size at multiple spatial scales whilst taking in to consideration other landscape characteristics.

Pipistrellus spp. and *E. serotinus* are more opportunistic foragers compared with the other species studied here, often taking advantage of insects around streetlights (Table 1.1., though see Mathews *et al*., 2015) and so those species would be expected to tolerate landscapes with higher light levels. Consistent with this hypothesis, we found roosts of *P. pipistrellus*, *P. pygmaeus* and *E serotinus* had significantly higher light levels at roosts than *M. nattereri* and *R. hipposideros* and *P. auritus*. In addition, *P. pipistrellus* and *P. pygmaeus* had significantly higher light levels than *P. auritus. R. ferrumequinum* was not found to have significantly lower light levels than *Pipistrellus spp.* and *E. serotinus*, however it is likely that this is due to the low sample size (n= 30) as mean light levels across roosts were lower than all species bar *R. hipposideros.*

Although there were apparent differences in landscape light exposure amongst species, these differences accounted for low levels of variation ($R^2_{GLMM(m)}$ = 0.056). The combined random and fixed effects, however, explained large amounts of variance ($R^2_{GLMM(b)}$ = 0.988). Alongside other sources of variation, the random effect of region was included as, for example, south-east England has high levels of light pollution so species with distributions extending to these regions may have high light readings as an artefact of their range rather than light tolerance.

If light has a direct negative effect on bat populations, it is important to have an understanding not only of their level of exposure but also what the relevant trends in

artificial lighting are. Although there were significant trends for some species and regions (Appendix Table 2.5), these were all small changes. Changes of a value of around 3 DMSP-OLS units over a 10-year period are likely to represent true changes in light levels from developments such as a new housing estate or roads (Bennie *et al.*, 2014a). Here the changes detected were of a much lower magnitude, 15-20 times less (e.g. *R. hipposideros* roosts had an estimated decrease of 0.02 light units per year and *P. pipistrellus* roost light levels increased by 0.01 per year) and so likely to be artefacts of the dataset rather than true changes in light levels. This is encouraging as it suggests that light levels are relatively stable at the landscape level and so light management could be focus on individual developments where roosts are known.

The use of satellite imagery to evaluate the impacts of light pollution on biodiversity is appealing as it provides large and spatially extensive datasets and can be used to investigate temporal patterns of change (Kamrowski *et al*., 2014; Gaston *et al*., 2015a). There are, nonetheless, some limitations. Satellite images capture upwards light spill and so only one metric of illumination, although this has been found to correlate well with others. Resolution is also an issue, with the long-term DMSP-OLS dataset only available at coarse resolution (3km), and the and the higher resolution Suomi NPP dataset (300m) not yet available over a long period.

This research highlights the potential to use satellite imagery to understand bat roost locations. We demonstrate that landscapes around bat roosts typically have higher levels of artificial lighting than random locations and so it may be other factors that are more important to roost location than lighting. Despite this, there were differences between light profiles of species, with species that are considered of higher conservation importance

positioned in darker areas than more adaptable, lower conservation priority species. In addition, we demonstrate that larger roosts are found in darker areas than smaller roosts, however this may be correlated to other landscape features not considered here.

Chapter 3: Landscape-scale effects of street lighting

Thesis PP 65–85

3.1 Summary

Artificial light at night is a growing conservation issue. It alters the nighttime environment, disrupting the movements and behaviour of nocturnal animals. Despite these effects being studied in detail at local scales, they are rarely examined at landscape-level. For highly mobile organisms, landscape studies are important to understand the differential effects of artificial nighttime lighting at different habitats. Here we surveyed eight *Rhinolophus ferrumequinum* maternity roosts and their surrounding habitat in south-west England, to assess the combined effects of landscape features and street lighting on the spatial distribution of commuting and foraging bats. At each roost, 25 pairs of full spectrum acoustic detectors were deployed at randomly selected pairs of lit and dark locations in suitable habitat along roads in a 4 km radius. Most *R. ferrumequinum* passes (92.6%) were found at dark locations, with significantly higher bat activity at dark locations across different landscapes. Street light intensity (measure in µmol with a light sensor with peak sensitivity at 590.5 nm) was negatively associated with bat activity. Bat activity was significantly affected by the type of road the detector was placed on. Minor roads, which are typically narrow with low traffic levels, had higher bat activity than both A and B roads, which are associated with wider carriages and a higher traffic flow. Our study highlights how artificial nighttime lighting affects mobile organisms across a landscape and may reduce the value of otherwise important habitat features. Due to their high use, areas of the landscape important for commuting and foraging, such as those close to maternity roosts and low traffic roads, are likely to be more sensitive areas for bats in response to street lighting and should thus receive particular attention in lighting reduction schemes.

3.2 Introduction

Urbanisation has profound effects on animal behaviour, abundance, and distribution, and on species diversity (Mcdonald *et al.* 2008; Gaston 2010). One component of this modification has been the introduction of artificial lighting into the nighttime environment, and the resultant disruption of natural daily and seasonal cycles of light and dark (Rich & Longcore 2006; Hölker *et al.* 2010a; Gaston *et al.* 2013, 2014a, 2015b). By the beginning of the 21st Century, approximately one fifth of the global landmass experienced artificial nighttime lighting (Cinzano *et al.* 2001) and its extent is growing at an estimated 6% per annum (Hölker *et al*. 2010b). Most European countries are experiencing marked ongoing increases in nighttime brightness (Bennie *et al.* 2014a), and artificial nighttime lighting is prevalent even in areas protected for biodiversity (Gaston *et al.* 2015a). Artificial lighting can affect physiological processes (e.g. Dominoni *et al.* 2013; Poulin *et al*. 2013), timing of foraging (e.g. Larsen & Pedersen 1982; Bird *et al.* 2004; Santos *et al*. 2010; Becker *et al*. 2013; Dwyer *et al*. 2012), daily movements (e.g. Moore *et al*. 2000; Stone *et al.* 2009; Riley *et al*. 2012), migratory behaviour (e.g. Evans *et al*. 2007; Poot *et al*. 2008; Riley *et al.* 2013), reproductive behaviour (e.g. Miller 2006; Kempenaers *et al*. 2010; Titulaer *et al*. 2012; van Geffen *et al.* 2015), timing of mortality (e.g. Jones & Francis 2003; Rodríguez *et al*. 2012), population dynamics (e.g. Bennie *et al*. 2015; Sanders *et al*. 2015), and ecosystem processes/services (e.g. Lewanzik & Voigt 2014).

Many studies have documented behavioural impacts of artificial nighttime lighting at local scales using point sampling under single lights or a string of lights (e.g. Stone *et al.* 2009; Kempenaers *et al.* 2010; van Langevelde *et al.* 2011; Davies *et al.* 2012; Perkin *et al.*

2014). However, the way in which lighting influences the use of landscapes by animals remains poorly understood (but see Beier 1995). For highly mobile species, some areas of the landscape within their foraging range clearly have more ecological value than do others, and the importance of lighting may therefore vary between habitats. Difficulties in measuring such impacts include the need for replication of both individuals and landscapes. One way to address this is through systematic sampling across lit and unlit habitat features in multiple landscapes.

Most bats are nocturnal (Bennie *et al.* 2014c) and so are particularly vulnerable to artificial nighttime lighting. Their high mobility means that a landscape scale approach is required to understand these impacts. It is clear artificial nighttime lighting can reduce the activity of slow flying bats at local sites (Rydell 1992; Stone *et al.* 2012; Lacoeuihe *et al.* 2014). But it seems likely that the scale of the effect will be modified by the precise location of artificial nighttime lighting given that different habitat patches have varying levels of importance as a resource to bats (Avila-Flores & Fenton 2005). Evidence from radio-tracking suggests that areas of high importance to bats tend to be close to roosts, flyways and foraging grounds (e.g. Entwistle *et al.* 1996; Reiter *et al.* 2012). Pivotal flyways for many bat species are likely to be associated with landscape features such as treelines, hedgerows and streams (Walsh & Harris 1996; Dietz *et al.* 2013) At sites close to maternity roosts, artificial nighttime lighting can disrupt commuting (Stone *et al.* 2009, 2012) and delay emergence (Downs *et al.* 2003; Boldogh *et al.* 2007), but the impact of artificial nighttime lighting on the use of these key habitat features has been little investigated. Likewise, the effects of artificial nighttime lighting on areas used for foraging have received little attention, although

comparisons have been made of feeding rates at streetlights and at sites away from them (Rydell 1992; Lewanzik & Voigt 2014).

Here we determine the impact of artificial nighttime lighting on the use of habitat features at a landscape scale. We use the light sensitive bat species *Rhinolophus ferrumequinum* as a case study, focussing on its activity patterns around maternity roosts. It is of high conservation concern across Europe, with measures to protect the foraging and commuting areas for key populations being included in the European Habitats Directive, 1992/42/EEC (Annexe II). We explore if the short term negative effects of street lighting on behaviour seen in the closely related *R. hipposideros* (Stone *et al.* 2009, 2012) persist when *R. ferrumequinum* is exposed long-term to permanent street lights. We hypothesise that if *R. ferrumequinum* exhibit light avoiding behaviour there will be less bat activity at street lit locations compared with dark locations. We then examine the effect of light spectra on *R. ferrumequinum* bat activity with the hypothesis that shorter wavelengths will have a greater negative effect on bat activity than loner wavelengths. Finally, to test whether habitat features differ in sensitivity to artificial lighting for bats (due to their importance for bats), we hypothesise that the closer a favourable habitat feature is to light, the stronger the negative effect will be on bat activity compared with less favourable habitat features.

3.3 Materials and methods

3.3.1 Study area

Eight *R. ferrumequinum* maternity roosts were surveyed in south-west England from 25th April – 24th June 2013, during the period when these roosts were established but before parturition. Roosts were selected because they (i) had large populations (>90 individuals) to

provide a reasonable probability of detecting bat activity of this rare species in the landscape; (ii) had surrounding areas comprised of a matrix of lit and unlit sites; and (iii) were distributed across the range of *R. ferrumequinum* in England (Figure 3.1).

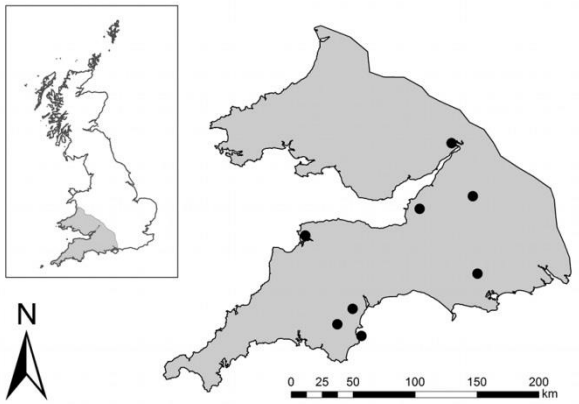


Figure 3.1 *Rhinolophus ferrumequinum* roost locations in solid circles shown in UK range (IUCN 2008g) in light grey. Inset image of range within Britain.

3.3.2 Survey design

The landscape was surveyed within a radius of 4 km of each roost, representing the area where most bat activity is likely to be concentrated (Table 2.1). These zones were characterised by having large areas of arable and horticultural ground, improved grassland and broadleaf woodland (see Table 3.1 for main characteristics by site). It was not possible to determine if part-night lighting schemes were operational during the time of the study. Areas <500 m from the roost were not surveyed as it could be more difficult for animals to exhibit habitat selection at such close proximity to the point of emergence. Beyond this distance, within the sustenance zones of each roost, 25 random points at least 200 m apart were generated using ArcMap 10 (ESRI Inc. 2006). At each point, a full spectrum bat detector (SM2BAT/SM2BAT+, Wildlife Acoustics, Concord, MA, USA) equipped with an

omnidirectional microphone on either a 2 m or 10 m cable was placed along a roadside at the nearest streetlight in suitable habitat. Suitable habitat was defined as a hedgerow or treeline that a bat might commute along (as seen in *R. hipposideros*; Schofield 1996). Each lit detector was paired with one at a dark location in similar habitat at least 100 m away whilst still on a road, making a total of 50 bat detectors for each roost (see Figure 3.2 for an example of detector deployment). The location of each detector were recorded with a Garmin Vista HCx and, as necessary, later more accurately using appropriate maps. Detectors were set to a sampling rate of 196kHz and recorded in a compressed format (WAC) from half an hour before sunset until half an hour after sunrise. Recordings were made for 5–8 continuous nights per roost. The total number of detectors per roost for which data were analysed was 43.1 ± 3.0 (mean ± SD), with a range of 36–47 depending on the failure rate of detectors.

Table 3.1 Summary of maternity roosts surveyed with location, 2013 roost size and dominant land class. For each roost, the top three dominant (by %) land classes (derived from Land Cover Map 2007 data) are given with % values.

Roost	County	2013 roost size	Dominant land classes in 4km radius of roost (%)
1	Devon	1631	Arable and horticulture (38.38) Improved grassland (33.77) Broadleaved, mixed and yew woodland (17.96)
2	Wiltshire	131	Improved grassland (42.49) Arable and horticulture (36.10) Broadleaved, mixed and yew woodland (9.59)
3	North Somerset	453	Improved grassland (40.77) Arable and horticulture (19.32) Broadleaved, mixed and yew woodland (14.04)
4	Devon	76	Arable and horticulture (38.53) Improved grassland (25.65) Broadleaved, mixed and yew woodland (19.79)
5	Gloucestershire	254	Coniferous woodland (24.76) Arable and horticulture (23.13) Improved grassland (17.99)
6	Mendip, Somerset	~ 120	Arable and horticulture (43.54) Improved grassland (34.37) Broadleaved, mixed and yew woodland (9.85)
7	Devon	~67	Arable and horticulture (28.41) Built up areas and garden (26.36) Improved grassland (20.19)
8	Devon	342	Improved grassland (49.60) Arable and horticulture (21.94) Built up areas and gardens (7.18)

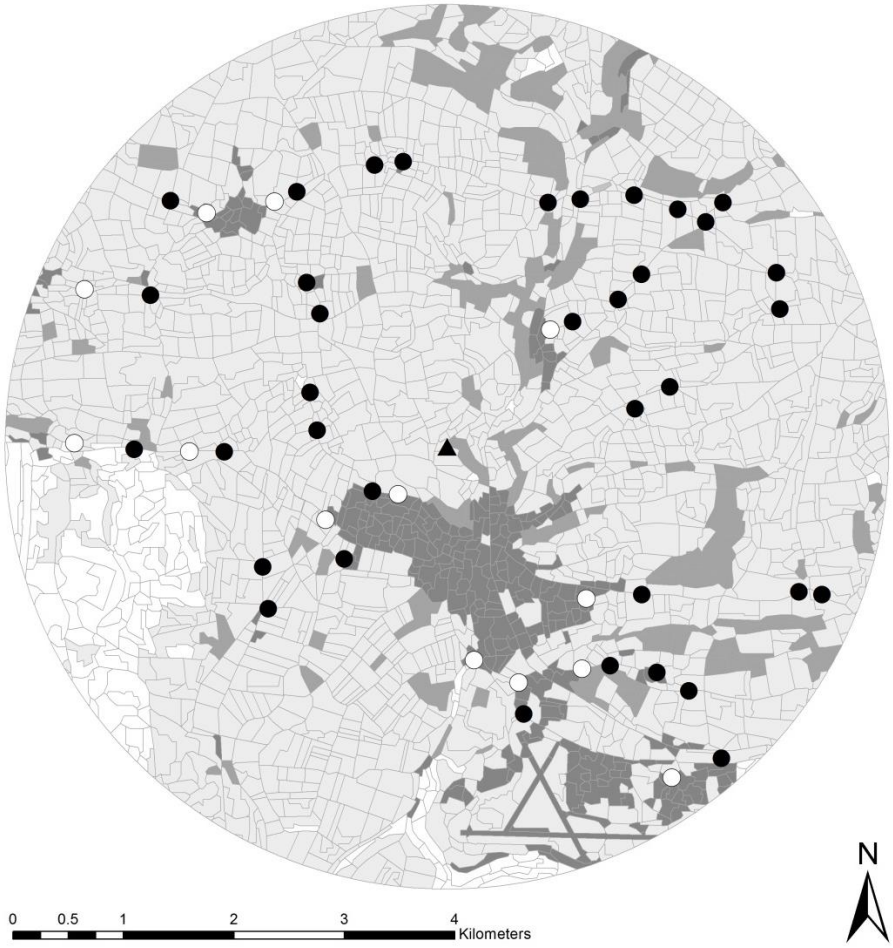


Figure 3.2 Detector deployment within a 4km radius of a roost. Solid triangle indicates the roost, solid circle the dark detector locations and open circle the street lit detectors. Habitat parcels are shown in different shades. These represent — from darker to lightest shades — urban, woodland, arable and grassland, and other habitats. Simplified from Centre for Ecology and Hydrology (CEH) Land Cover Map (LCM) 2007 data.

3.3.3 Habitat features

Distances between each detector and the nearest patch of freshwater, woodland, buildings and the main maternity roost were calculated. Habitat features were identified from Ordnance Survey Mastermap (EDINA Digimap Ordnance Survey Service) in ArcMap 10

(ESRI Inc. 2006). The road type where the detector was deployed was classified using the Ordnance Survey Meridian 2 dataset (EDINA Digimap Ordnance Survey Service). Roads were categorised as A, B or minor: A roads are typically wide roads with large amounts of traffic, B roads tend to have high traffic flow but less than A roads, and minor roads are often narrow with low levels of traffic (Department for Transport, 2012).

3.3.4 Light readings

Light readings were taken at each sampling point between December 2014 and January 2015 using an eight channel broadband light sensor (SpectroSense light meter, Skye instruments, Powys, UK) mounted on the top of a car; lighting patterns in the landscapes were stable between the period of the bat survey and this season. Light readings were recorded every two seconds, with the following wavelength sensitivities: ultraviolet A (UVA), violet, blue, green, orange, red, far red and lux (see Table 3.1 in the Appendix for peak sensitivities). The car was driven at a speed as close as practicable to 10 miles/hour. Maximum light readings were extracted in ArcMap 10 from a 30 m radius of each bat detector location.

3.3.5 Sound analysis

Sound files from the bat detectors were converted from WAC to WAV format using Kaleidoscope Pro (v. 1.1.20, Wildlife Acoustics, USA) to filter all sound outside the range of 16–120 kHz and remove pulses outside 2–500 ms. The remaining files were processed within the same software using automated species classification (Bats of the United Kingdom v.1.0.5). All sonograms identified as *Rhinolophus spp.* or with no identification were manually verified using the Kaleidoscope Pro sonogram viewer. Bat passes were

identified to species level for *Rhinolophus spp.* using established parameters for call amplitude and duration (Russ 2012).

Bat activity was defined as bat passes per detector per night. A bat pass was classified as at least three bat pulses with less than a second between pulses. Multiple passes were recorded in a file if pulses were distinguishable at different frequencies or if there was a break of at least one second between pulses.

3.3.6 Statistical analysis

To assess whether there were more bat passes per night at street lit or dark detectors, a generalized linear mixed model (GLMM) with a negative binomial error structure was fitted to account for overdispersed count data. Streetlight was specified as a fixed effect with two levels (presence/absence). Detector nested within roost was defined as a random effect to account for repeated nights at the same detectors and the same bat roost. As bat activity is strongly affected by weather conditions, a feature that will vary similarly across all detectors around a given roost, night was fitted as a random effect.

To compare the light readings at dark and street lit detectors, linear models were fitted with light reading as the response variable and streetlight presence or absence as a predictor. A Gaussian distribution was specified to account for continuous data with a normal distribution of residuals. Separate models were constructed for each of the eight light readings taken.

To investigate the effects of light intensities within different spectrum ranges on nightly bat activity, a GLMM was fitted with a negative binomial error structure. Eight light readings were included as predictors instead of the fixed effect of streetlight presence or absence. A random effect of detector nested within roost and a random effect of night was specified.

For these analyses, data on light readings were missing for 6 of the 345 detectors. To determine whether the simple presence/absence of streetlights, or the intensity of light of varying spectral composition was a better predictor of bat activity, the AIC values of the two models (using the same error structure and excluding detectors with missing light spectrum data) were compared. After comparing the AIC values between these two models, it was determined that streetlight presence was a better predictor of bat activity than the light readings, and so this predictor was used for further models.

To test the combined effects of street light presence or absence and habitat features on bat activity, a negative binomial GLMM was fitted. Night, and detector nested within site were specified as random effects. Road type, distance to roost, freshwater body, woodland and building were included as fixed effects. Two-way interactions were fitted for all habitat features and streetlight presence or absence. A *post-hoc* Tukey's test was used to compare bat activity between different road types.

Explanatory variables were rescaled to a mean of zero before inclusion in models to improve model convergence. For all models, the variables included in the final minimum adequate models were selected using a backwards step-wise model simplification approach. *F*-tests were performed, comparing simplified models with previous models, using a threshold of $p<0.05$ for inclusion in the final model (Crawley 2007). Model averaging approaches were not used because the error structure of the model was not compatible with this approach the technique. Models predicting bat passes were initially run with Poisson error structures and then negative binomial error structures, using AIC values to determine the best fit and to select the error structure. Statistical analyses were performed with R (v 3.0.3) using the package lme4 (v 1.1-7) to fit GLMMs, the base package stats (v

3.0.3) to fit linear models with a Gaussian error structure and multcomp (v 1.3-3) to perform *post-hoc* Tukey's tests.

3.4 Results

A total of 1,710 *R. ferrumequinum* bat passes were recorded across 345 detector locations. Most (92.6%) bat passes were recorded at dark detectors. Street light presence had a significant negative effect on bat passes (X^2 = 25.26, *d.f.* = 1, p<0.001) (Figure 3.3).

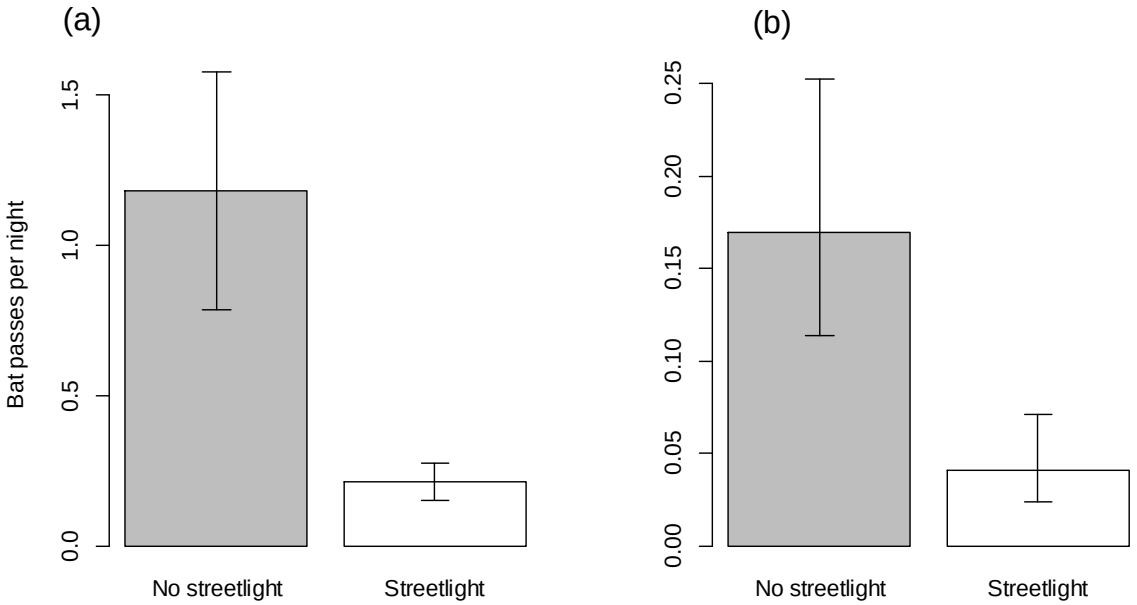


Figure 3.3 Nightly bat passes with 95% confidence intervals at dark and street lit locations across sites and detectors from (a) the raw data and (b) model predictions accounting for variation across detectors within sites and nights.

Of the eight light reading predictors fitted to explain bat activity, only one sensor with a peak frequency sensitivity of 590.5 nm (corresponding to orange light) was retained in the final model. Orange light was negatively correlated with bat passes (X^2 = 19.84, *d.f.* = 1, p<0.001). Orange light levels were highly correlated (values above 0.7) with the green, red

and lux predictors (see Appendix Table 3.2 for correlation matrix). Street lit detectors had significantly increased intensities for most of the recorded wavelengths compared to the dark detectors (p<0.001) and significantly higher values for violet readings (p<0.05). However, no significant differences were found for UVA readings between street lit detectors and dark detectors (p = 0.28) (Table 3.2).

Table 3.2 Predicted differences in light levels taken at dark and street lit detectors across detectors and roosts obtained from models. Predicted values are given with lower and upper 95% CI in brackets below. Measurements are given in µmol except for Lux which is given in lx and UVA which is given in mW/m2.

Spectrum	Predicted value		Comparison of lit and dark detectors	
	Dark detectors	Lit detectors	*F* statistic	*P*-value
Lux	0.143	20.484	$F_{1,393}$ = *191*.3	<0.001
	(-1.497,1.782)	(18.103,22.866)		
UVA	3.225	3.331	$F_{1,393}$ = 1.2	0.28
	(3.115 ,3.336)	(3.171,3.492)		
Red	0.000	0.010	$F_{1,393}$ = 89.9	<0.001
	(-0.001,0.001)	(0.009,0.012)		
Far red	0.000	0.003	$F_{1,39}$ = 48.5	<0.001
	(0.000,0.001)	(0.002,0.004)		
Violet	0.013	0.019	$F_{1,393}$ = 3.9	<0.05
	(0.010,0.016)	(0.014,0.023)		
Blue	0.008	0.019	$F_{1,393}$ = 35.1	<0.001
	(0.005,0.010)	(0.016,0.022)		
Green	0.005	0.032	$F_{1,393}$ = 118.3	<0.001
	(0.002,0.008)	(0.028,0.036)		
Orange	0.005	0.151	$F_{1,393}$ = 175.7	<0.001
	(-0.007,0.018)	(0.133,0.169)		

The final model incorporating habitat features included the following variables: streetlight presence (X^2 = 25.73, *d.f.* = 1, p< 0.001), roost distance (X^2 = 9.53, *d.f.* = 1, p<0.005) and road type (X^2 = 7.45, *d.f.* = 2, p<0.05). With increasing distance from a roost, bat activity was reduced. Bat activity was highest at minor roads compared with both A and B roads *(p* = 0.08 and p = 0.09 respectively) (Figure 3.4).

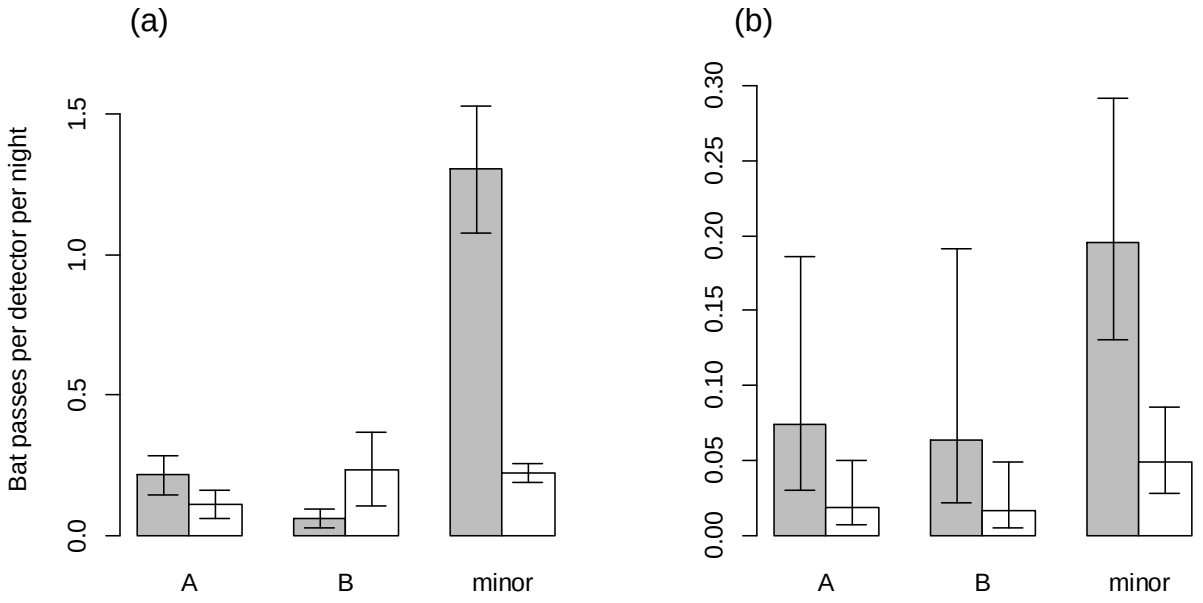


Figure 3.4 The effect of road type on bat activity. Bars represent bat activity at dark (grey bars) and street lit (white bars) sites with 95% CI error bars with (a) the raw data (b) model predictions accounting for variation across detectors within sites and nights.

3.5 Discussion

Worldwide, 54% of human populations currently live in urban areas and the number of people in urban areas is predicted to increase from 2014 to 2050 by 2.5 billion (UN, 2015). Urbanisation has many associated effects (Grimm *et al*. 2008) including high levels of nighttime lighting (Hale *et al*. 2013). Our analyses demonstrate that street lighting can have

negative impacts on bat activity across the landscape. This highlights the need for careful consideration of the placement of streetlights in the landscape for sensitive areas.

3.5.1 Road type

The results presented here are the first empirical evidence that bat activity varies according to road type, and has important conservation implications. It is consistent with modelled data of bat movements which have suggested that larger roads with greater traffic volume reduce bat activity (Bennett *et al.* 2013). A and B roads may have low bat activity due to higher levels of traffic (Zurcher *et al.* 2010) and associated noise (Schaub *et al.* 2008; Bennett & Zurcher 2013; Kitzes & Merenlender 2014) as well as larger roads representing wider crossing distances and thus creating landscape barriers (Fensome & Mathews 2016).

In the UK, there is no legal requirement to light roads; however, under the Highways Act 1980, County Councils have a duty of care to ensure safety on roads. Street lighting is used on roads to minimize risk of accident and crime and to limit the county council's liability. Areas of high risk are those with features such as junctions, pedestrians, parked cars and slow moving vehicles (The British Standards Institution, 2012). This results in minor roads, as classified in this study, in urban areas being likely to be lit. This highlights a clash between planning decisions to light roads and conservation needs to protect areas of high bat activity.

3.5.2 Spectral composition of light

Many of the globally installed street lights currently use a high pressure sodium type lamp; however, there is a rapid and widespread move underway to replace these lamps with more energy efficient, whiter lights such as LED lighting (Gaston 2013). Some of these newer

lights emit more blue light compared with high pressure sodium lighting, raising concerns about their ecological impact (Falchi *et al*. 2011; Gaston *et al.* 2012). In common with much of the UK, most street lights in our study areas were high pressure sodium and therefore short-wave length light emissions were similar across all lit areas, and no difference in UVA levels at dark and street lit locations were found. Insects are highly attracted to short wavelength lighting (van Langevelde *et al.* 2011; Somers-Yeates *et al.* 2013) and so street lights emitting UV may attract fast flying, light tolerant bats (as documented in a study of the impacts of conversion from low pressure sodium to metal halide lamps (Stone *et al.* 2015b)), however its effect on slow flying bats such as *R. ferrumequinum* is unknown.

In this study, a higher intensity of light emitted at 590.5 nm had a negative effect on bat activity and these light readings were highly correlated with green, red and lux readings. Orange light, in comparison to dark areas, has been shown to be negatively correlated with the occurrence of *Eptesicus serotinus*, but positively correlated with that of *Pipistrellus pipistrellus*, *P. pymaeus* and *P. kulii* (Lacoeuilhe *et al.* 2014). However, many commercially available street lights may have similar light profiles to each other and provide no difference in the effect on bat activity, as seen in Rowse *et al.* (2016).

3.5.3 Conservation implications

This study demonstrates that *R. ferrumequinum*, a slow-flying bat species, avoid street lit areas across the landscapes. We also highlight that street lighting can turn well-utilised habitat features into unused habitat features. The implications of these findings are that without careful consideration for placement of street lights, mobile organisms' commuting routes and foraging efficiency may be disrupted. Several strategies have been suggested to

mitigate the impacts of street lighting (see Gaston *et al*. 2012) and given the results presented here, it would be advisable in sensitive areas to prevent the placement of new lights, remove current lighting and avoiding trespass of light into these areas.

Chapter 4: Part-night lighting: Implications for bat conservation

Published as: Day, J., Baker, J., Schofield, H., Mathews, F. and Gaston, K. J. (2015). Part-night lighting: implications for bat conservation. *Animal Conservation*, 18, 512-516.

Thesis PP 85–96

4.1 Summary

Artificial nighttime lighting has many effects on biodiversity. A proposed environmental management option, primarily to save energy, is to alter the duration of night lighting. Using the greater horseshoe bat *Rhinolophus ferrumequinum* as an example of a photophobic species, we explored roadside behaviour patterns throughout the night to assess the potential impact of part-night lighting. We found a large primary peak in activity 1 h after sunset, followed by a smaller secondary peak before sunrise. Simulated part-night lighting scenarios reveal that to capture a large proportion of bat activity, streetlights should be switched off before midnight. Current proposed uses of part-night lighting are unlikely to capture natural peaks in activity for nocturnal species.

4.2 Introduction

Artificial nighttime lighting, predominantly through street- lights, places significant pressures on the natural environment (Rich & Longcore 2006; Perkin *et al.* 2011; Gaston *et al.* 2013; Davies *et al.* 2014). Light pollution is widespread, through direct lighting and skyglow over large areas, and is closely associated with urbanization, the globally fastest growing land use change (Imhoff *et al.* 1997; Sutton 2003). It is also known to have biological impacts spanning from the molecular to community level (Davies *et al.* 2012; Gaston *et al.* 2013) and to have marked influences on physiology (Navara & Nelson 2007), behaviour (Bedrosian *et al.* 2011), movements (Baker 1990), reproduction (Kempenaers *et al.* 2010) and mortality (Le Corre *et al.* 2002). Such effects have been documented for a wide diversity of organisms (Gaston *et al.* 2013) (including plants, insects, fish, amphibians, reptiles, birds, rodents, bats and primates).

Several policy and management responses to the impacts of artificial nighttime lighting have been proposed (Gaston *et al.* 2012). These include (1) protecting existing dark spaces; (2) creating new dark spaces; (3) altering the spectrum of artificial lighting; (4) reducing artificial light trespass; (5) dimming of artificial lighting; (6) part-night lighting. Part-night lighting involves streetlights being switched off during periods of the night when human activity is low. This approach is being employed widely across Europe (Bennie *et al.* 2014a) principally motivated not by environmental considerations but by the need to cut public expenditure and reduce carbon emissions (Gaston 2013).

The extent of environmental benefits from part-night lighting can be debated. Many ‘nocturnal’ species may have peaks of activity towards dawn and dusk, so the benefits may

be limited as lighting is often operational during these hours under part-night lighting schemes (Gaston *et al.* 2012). Bats are one of the largest groups of nocturnal mammals and artificial lighting can have profound influences on their behaviour (e.g. Stone *et al.* 2009). However, understanding of their activity times is heavily biased towards emergence from roosts (Bullock *et al.* 1987; McAney & Fairley 1988; Duvergé *et al.* 2000) or limited foraging data from few sites and individuals (Rydell *et al.* 1996).

Here we analyse the hourly activity patterns of *Rhinolophus ferrumequinum* throughout the night, using data collected at unlit locations in Chapter 3. From this data we establish if there are any peaks in activity. We then explore if these activity patterns are likely to benefit from part-night lighting schemes (with benefits defined as <50% activity during the dark portion of the night). *R. ferrumequinum* makes a valuable case study as it belongs to a genus of photophobic bats (Chapter 3; Korine & Pinshow 2004; Stone *et al.* 2009, 2012) and is of conservation concern within Europe [with an estimated UK population of > 9300 individuals based on known maternity roosts (Joint Nature Conservation Committee, 2013) and listed under Appendix II of the European Habitats Directive, 1992/42/EEC].

4.3 Material and methods

We determined the hourly activity patterns of *R. ferrumequinum* using acoustic surveys as described in Chapter 3, during in late April–June 2013. This coincided with the pre-birth period (Ransome & McOwat 1994). The sustenance zones (500 m to 4 km radius) (Dietz *et al.* 2013) of eight *R. ferrumequinum* maternity roosts in south-west England (Figure 3.1) were intensively sampled with acoustic surveys. A subset of the detectors analysed in

Chapter 3 was used, by selecting only dark detectors. Detectors were randomly placed in roadside hedges at least 100 m from an artificial lighting source, representing bat activity potentially at risk to light pollution. An average of 32 ± 1.3 (mean ± se) full-spectrum bat detectors (SM2BAT, Wildlife Acoustics, Concord, MA, USA) were deployed for 5–8 nights per roost. Numbers of detectors per site were determined by the number available at deployment (ranging from 27 to 38 detectors).

As in Chapter 3, sonograms of bat calls were processed using Kaleidoscope Pro (v.1.1.20, Wildlife Acoustics) with British bat classifiers (v.1.0.5). All bat passes identified as *Rhinolophus spp.* and those with no identification were manually verified using established call parameters (Russ, 2012).

To identify peaks in nightly activity, differences in hourly bat passes throughout the night were modelled using generalized linear mixed models (GLMMs) on untransformed data (O'Hara & Kotze 2010). Hours after sunset was fitted as a categorical fixed factor. Random effects of site, detector and night were specified in order to account for spatial and temporal autocorrelation. A Poisson error structure was fitted with a log link function. To improve model fit, the ninth hour of the night, which was only present at some sites, was removed as well as detectors with no bat activity. The mean (±se) number of detectors analysed per site was 16.75 (±2.08), range = 11–26. A Tukey's *post-hoc* test was performed to determine significance levels (adjusted *P*-values) between hour groups. An additional model was fitted with hours before sunrise as the categorical fixed factor. The additional model was used to explore how differing night lengths throughout the sampling period (mean ± se = 8 h 10 min ± 6 min, range = 7 h 28 min–9 h 32 min) may reduce the perception of a pre-dawn peak when using the variable hours after sunset.

To assess the potential effects of part-night lighting schemes, different light regime scenarios were explored, altering the time when the streetlights could be switched off, in line with likely part-night lighting policies. Hourly bat passes were aggregated into two sections of the evening. The first section was classed as light, representing bat activity potentially exposed to streetlights, and the remainder as dark. The start time of the dark period of the night changed for each scenario. For the scenarios, the dark portion start time was altered from 10 pm to 5 am with an increment of 1 h, creating eight part-night lighting scenarios. As a measure of potential impacts of part-night lighting, in each lighting scenario, total nightly bat activity was compared during the dark and lit period with separate GLMMs for each scenario, fitted with negative binomial error structures and detector nested in site as random effects. The potential proportion of bat activity captured during the dark period of the night was used as a measure of how effective the lighting scenario was.

All statistics were performed with R (v.3.0.3) using the packages lme4 (v.1.1–7) to fit Poisson GLMMs, glmmADMB (v.0.7.7) to fit negative binomial GLMMs and multcomp (v.1.3-3) for post-hoc Tukey's tests. Models were evaluated for fit by calculating marginal R^2 ($R^2_{GLMM(m)}$) and conditional R^2($R^2_{GLMM(c)}$) (Nakagawa & Schielzeth 2013). $R^2_{GLMM(m)}$) represents the variance explained by the models' fixed terms and $R^2_{GLMM(c)}$ by the combined fixed and random terms. Additionally, fit was measured by calculating pseudo-R^2 (R^2_N) (Nagelkerke 1991).

4.4 Results

A total of 1563 greater horseshoe bat passes were recorded at 134 sampling points over a span of 50 unique nights. Bats were active throughout the whole night with two distinct peaks. The first occurred 1–2 h after sunset. Activity was highest 1 h after sunset compared with all other hours apart from the second, sixth and seventh hour after sunset (p<0.01; Figure 4.1). A second peak in activity occurred during the sixth and seventh hour after sunset. Activity was lowest compared with all other hours immediately after sunset (p<0.01). The bimodal peak pattern was consistent at varying distances from the roost but with a reduced primary peak at 2–3 km from the roost and no secondary peak at over 3 km (see Appendix Figure 4.1). The model fitted accounted for half the variance in the data ($R^2_{GLMM(m)}$ = 0.17,$R^2_{GLMM(C)}$ = 0.49,R^2_N = 0.14). In the additional model, with hours before sunrise fitted as the explanatory variable, the morning peak in activity occurred at 1–2 h before sunrise in a similar morning pattern to the model fitted with hours after sunset as the explanatory variable (see Appendix Figure 4.2).

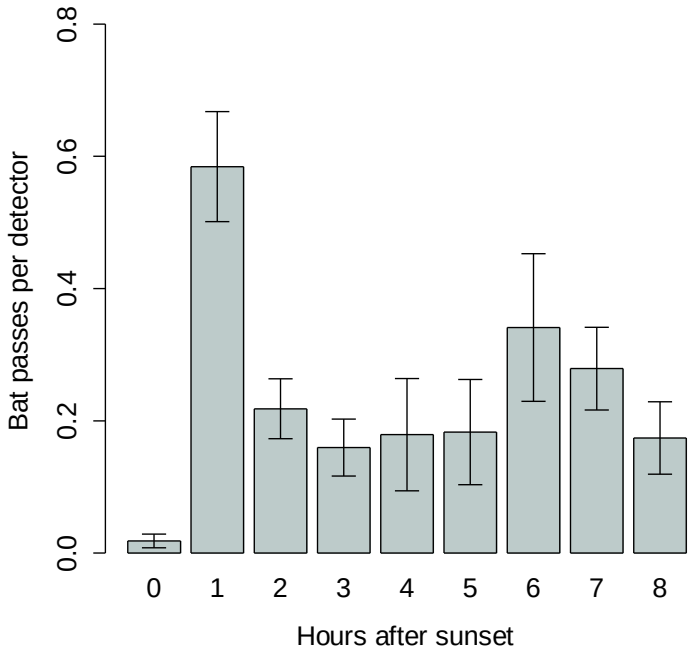


Figure 0.1 Mean hourly bat passes (±SE) across sites and detectors.

The eight part-night lighting scenarios varied in the level of bat activity captured from 81% with a switch off time at 10 pm to <1% when switching off lights at 5 am (Figure 4.2). Among the different part-night lighting scenarios, activity was only significantly higher in the dark portion of the night when lights were switched off before 11 pm. With a switch off time at midnight, the bat activity capture in the potential dark period fell to 46% with no significant difference during the lit and dark portion of the night. Switching the lights off beyond midnight failed to capture the majority of bat activity, with significantly higher numbers of bat passes during the potentially lit portion of the night.

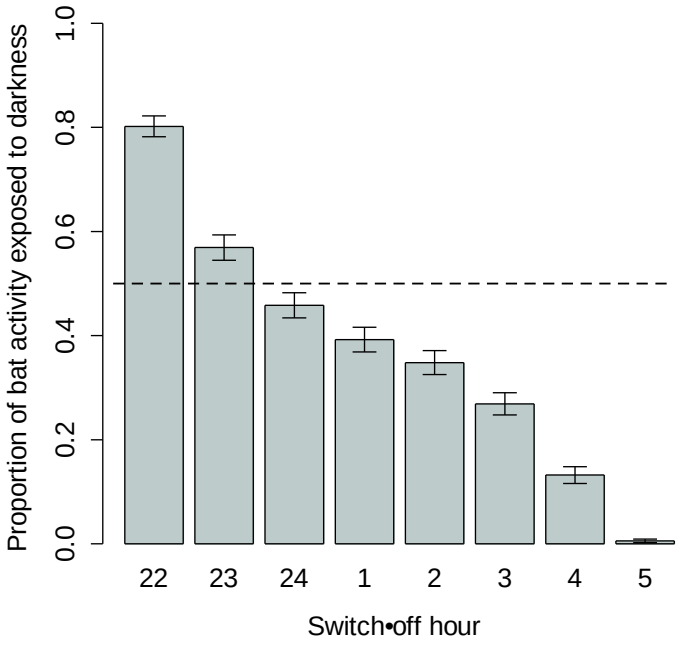


Figure 0.2 Proportion of *Rhinolophus ferrumequinum* activity potentially exposed to dark conditions within part-night lighting scenarios. Mean proportions of activity (±SE) across sites and detectors. A dashed line represents 50% bat activity in the dark portion of the night.

4.5 Discussion

With growing recognition of the financial costs and environmental impacts of artificial nighttime lighting, a variety of approaches are being explored to limit its use (Falchi *et al.* 2011; Gaston *et al.* 2012). Part-night lighting is an attractive management option, producing immediate energy and carbon emission savings; it is achievable through a variety of mechanisms and has limited impacts on humans. However, there are concerns, more often perceived than evidenced by empirical data, of increased risks of crime and of vehicle accidents (Gaston *et al.* 2014b). Part-night lighting schemes therefore often restrict switch

off to after midnight. The present study demonstrates a clear case in which the benefits of realistic part-night lighting schemes to a photophobic bat species would be limited.

The distinct bimodal activity pattern for *R. ferrumequinum* in the roadside environment documented here, which is not benefitted by part-night lighting, may be due to fluctuations in temperature governing prey availability (Rydell *et al.* 1996). This pattern in activity is likely to be widespread among nocturnal organisms either because they respond directly to changes in temperature or because they respond to activity patterns of prey. Examples of other insectivorous bats that have been documented with similar bimodal patterns include *Myotis spp.* at two riparian sites in Oregon (Hayes 1997); however, there can be variations in nocturnal patterns exhibited among and within species (Skalak *et al.* 2012). These variations are likely to be linked to the stages of the breeding cycle, with a more bimodal activity pattern seen in mid-pregnancy. It has been observed in *Eptesicus serotinus* that the secondary peak was pronounced during mid-pregnancy but lost or reduced during other stages (Catto *et al.* 1995). Part-night lighting is a valuable approach to reducing the costs and emissions of artificial lighting. However, for photophobic bats, alternative management approaches may provide greater benefits. These are likely to include more careful consideration of the positioning of streetlights (including their removal, in order to keep intact dark corridors for commuting), reductions in the trespass of light (particularly the horizontal emissions, reaching far distances) and the use of light spectra with longer wavelengths (Gaston *et al.* 2012).

Chapter 5: A before and after study on the effects of part-night lighting on bats

Thesis PP 97–114

5.1 Summary

Artificial nighttime lighting is increasing rapidly and its effects on biodiversity are a conservation concern. Part-night lighting is being introduced in many areas, limiting the duration of street lighting to reduce financial expenditure and carbon emissions. However, there may also be benefits to biodiversity. Here we present a before-after control study that evaluated the impacts of this change to part-night lighting on bats. Bat activity was monitored acoustically using cycled transects throughout the night. Following the change from full-night lighting to part-night lighting, we found a significant reduction in bat activity for *Pipistrellus pipistrellus* and a significant increase for *P. pygmaeus* and *Nyctalus noctula*. Most bat passes were recorded during the surveys at early periods of the night that remained light both before and after the change in lighting regime. Part-night lighting changes species activity levels compared with full-night lighting, however these impacts are limited by the timing of part-night lighting.

5.2 Introduction

Globally, human activities are causing large losses in species diversity (13.6%) and abundances (10.7%) (Newbold *et al.* 2015). More than half of the world's human population now lives in urban areas (UN, 2015) so it is a major concern for wildlife (McKinney 2002). Street lighting is ubiquitous in urban areas (Hale *et al.* 2013) because of the range of social and other benefits it brings (Gaston *et al.* 2014b). Until recently, the potential environmental impacts associated with such artificial nighttime lighting were rarely considered. There is now growing evidence that artificial nighttime lighting has many effects on wildlife (Longcore & Rich 2004) spanning from the molecular (Ouyang *et al.* 2015; van Geffen *et al.* 2015) to the community level (Davies *et al.* 2012; Davies *et al.* 2017). This has led to several mitigation options being proposed, including the maintenance and creation of naturally dark spaces, dimming lighting, part-night lighting, and changing the spectrum of artificial lighting emissions (Gaston *et al.* 2012). However, the effectiveness of these different options remains poorly understood.

Many local governments across the UK, and elsewhere around the world, have adopted regimes of part-night lighting. Here, street lights are switched off when the roads are quietest during the night, usually being turned off around midnight and back on before dawn (Stone *et al*. 2015a). This strategy is primarily being deployed to save energy whilst having minimal negative effects on safety and crime (Steinbech *et al.* 2015). Part-night lighting may only offer limited benefits to wildlife as many organisms exhibit peaks in activity shortly after sunset and before sunrise; typically, the periods when lights remain on (Gaston et al. 2012; Chapter 4). However, published empirical evidence of the effects remains extremely limited (Azam et al. 2015; Chapter 4).

Bats are one of the largest groups of nocturnal vertebrates, and many are known to be light averse. Mitigation for artificial nighttime lighting is therefore a high conservation priority. Street lighting is known to affect many aspects of bat biology and ecology, from disrupting circadian rhythms (Downs *et al.* 2003; Boldogh *et al.* 2007), to changing foraging behaviour (Rydell 1992) and disturbing commuting routes (Stone *et al.* 2009; Stone *et al.* 2012). The impacts of street lighting on bats vary between species, reflecting differences in flight characteristics and foraging behaviour. Fast-flying, aerial hawking species of insectivorous bats have been documented foraging around street lighting (Rydell 1992) taking advantage of the insects attracted to light. For these species, a reduction in lighting through part-night lighting may reduce foraging opportunities and in turn reduce bat activity. In contrast, slow-flying bat species tend to avoid lit areas at night (Stone *et al.* 2009*,* 2012). Part-night lighting may be particularly beneficial for these species in reducing their exclusion from areas of the landscape by street lighting. In line with these predictions, in an experimental set up of single street lamps in France under full-night lighting and part-night lighting, part-night lighting reduced the activity of *Pipistrellus pipistrellus*, a species known to forage around street lights and increased the activity for the light avoiding species *Plecotus spp.* (Azam *et al.* 2015).

Here, we conducted a before-after control-impact study of part-night lighting effects on bat activity. We monitored the implementation of part-night lighting across Devon, England. To establish bat activity throughout the night under full-night lighting conditions, we conducted acoustic surveys at sites before the installation of part-night lighting. These sites were then resurveyed the following year under part-night lighting. We examine if there is an effect of part-night lighting on bat activity and if this differs between bat species that

take advantage of insects and those that avoid street lit areas. We hypothesise that bat species which take advantage of insects around street lights will have higher bat activity on nights will all-night lighting compared with part-night lighting but that this trend will be reversed for bat species which avoid street lit areas.

5.3 Material and Methods

5.3.1 General methods

Bat activity was monitored during June–September of 2013 and 2014 at 21 sites across Devon in southwest England (Figure 5.1). Treatment sites (*n* = 17) had full-night lighting in 2013 and part-night lighting in 2014 whilst control sites (n = 4) had full-night lighting through both survey years. Each site was surveyed for one night in 2013 and again at a similar time of year (8.5 ± 1.7 (mean ± SD) days apart) and under similar weather conditions for a second night in 2014 (see Appendix Table 5.1 for survey dates). To capture activity throughout the night, sites were surveyed at four periods during both years: P1 at sunset, P2 halfway between sunset and 2 am, P3 at 2 am when part-night light had commenced, and P4 halfway between P3 and sunrise (Table 1).

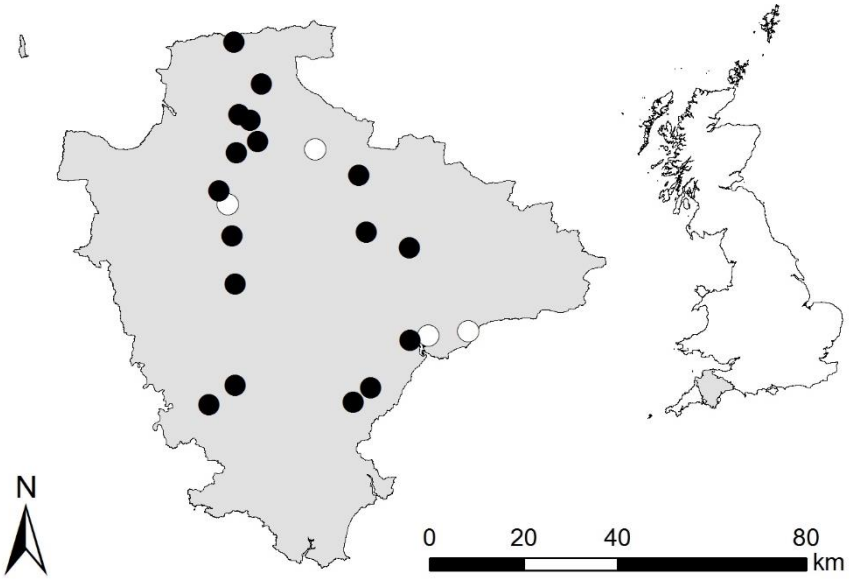


Figure 5.1 Study site locations within the UK and across Devon (shaded grey). Treatment sites are represented by solid circles and control sites by open circles.

Table 5.1 Street light levels at sites during survey periods over different survey years

survey period	survey start time	treatment site light level		control site light level
		year 1	year 2	year 1 & 2
P1	sunset	light	light	light
P2	between sunset and 2 am	light	light	light
P3	2 am	light	dark	light
P4	between sunrise and 2 am	light	dark	light

Bat activity was monitored with 15 minute transects cycled at a speed of ~15 km/hr (with mean ± SE speeds across transects of 12.76 ± 0.06 and a range of 8.62–16.73 km/hr). This speed was chosen to avoid sampling the same bat in a single location. The bicycle was assumed to have minimal impact on bat activity due to the low levels of light from the lights and low sound levels. Transects were repeated three times at each site during each survey period. Where towns were too small for a full 15 minute transect, the transects were curtailed at the end of the town and surveyed for less than 15 minutes. Surveys only covered areas that had high-pressure sodium streetlamps. Bat calls were recorded using a full spectrum bat detector (SM2BAT, Wildlife Acoustics, Concord, MA, U.S.A.) with a sampling rate of 196kHz and an omnidirectional microphone synchronised with a Global Positioning System device (Garmin eTrex Venture HC). Surveys were carried out on nights where weather conditions remained favourable throughout (defined as temperatures >8 °C, wind speeds <20 km/h, and dry). At the start of each transect, weather was checked using a handheld anemometer (EA 3010 Anemometer, Technoline Berlin, Germany). In the second year, additional cycle transects were carried out after P2 and P3 with a light meter (Spectrosense2, Skye Instruments, Powys, Wales, U.K.) mounted at a height of 1 meter from the ground. Measurements of light intensity and spectral composition were recorded before and after the lights were switched off (for details of the light measurements and sensors see Appendix Table 3.1).

All bat passes were manually identified by classifying sonograms using Kaleidoscope Pro viewer (Wildlife Acoustics). Species identification was based on established call parameters (Russ 2012). Where possible to distinguish, all calls were identified to species level apart from *Myotis spp.* calls, which were identified to genus. Where peak frequencies

of *Pipistrellus spp.* calls were between 49 kHz and 51 kHz, or 42 kHz and 43 kHz, calls were classified only to genus level. Bat passes were defined as at least two pulses of the same frequency and shape separated by a gap of less than one second between pulses (Fenton 1970).

5.3.2 Statistical analysis

For each species, Generalized Linear Mixed Models (GLMMs) with a Poisson error structure (to account for count data) were fitted to compare the number of bat passes in P3 and P4 between the lit surveys in 2013 and the dark surveys in 2014. The number of passes per transect was defined as the response variable. The predictor variables were an interaction term between part-night lighting regime (lights on or off) and period of the night, and site identity (specified as a random effect). Backwards step-wise model simplification was used to select minimum adequate models. *F*-tests were performed with a threshold of $p < 0.05$ to compare models with and without additional variables to select the final models (Crawley 2007). All statistics were carried out using R (v 3.0.3), using the package lme4 (v 1.1-7) to fit GLMMs.

5.4 Results

A total of 4,216 bat passes were recorded (742 at control sites and 3,474 at treatment sites) of seven species: *Barbastella barbastellus*, *Myotis spp.*, *Nyctalus noctula*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus* and *Rhinolophus hipposideros*. Forty-two nights were surveyed. *P. pipistrellus* and *P. pygmaeus* were present at all treatment and control sites. *P. pipistrellus* was present in both years for all sites surveyed while *P. pygmaeus* was not present at a 2013 night for a control and a 2014 night for a treatment site. *P. nathusii* was present at one site only, a treatment site during lit and dark surveys. *N. noctula* was present at three control sites and 12 treatment sites. *Myotis spp.* was found at one control site and 11 of the treatment sites. There were four bat passes for the rare and light sensitive light species *R. hipposideros* and *B. barbastellus*. These were all recorded during the dark sampling periods of year 2.

Total nightly bat passes recorded at treatment sites were higher during the part-night lighting surveys compared with full-night lighting for *N. noctula* and *Myotis spp.*, and were similar for the two for *P. pipistrellus* and *P. pygmaeus* (Figure 5.2). At the control sites, the numbers of bat passes were similar between survey years for *N. noctula* and *Myotis spp.*, however there were fewer *P. pipistrellus* and more *P. pygmaeus* during the second year of surveys. For *N. noctula*, *P. pipistrellus* and *P. pygmaeus*, survey period P2 had the highest number of bat passes followed by P3, P4 and then P1 (see Appendix Table 5.2 for full breakdown by species).

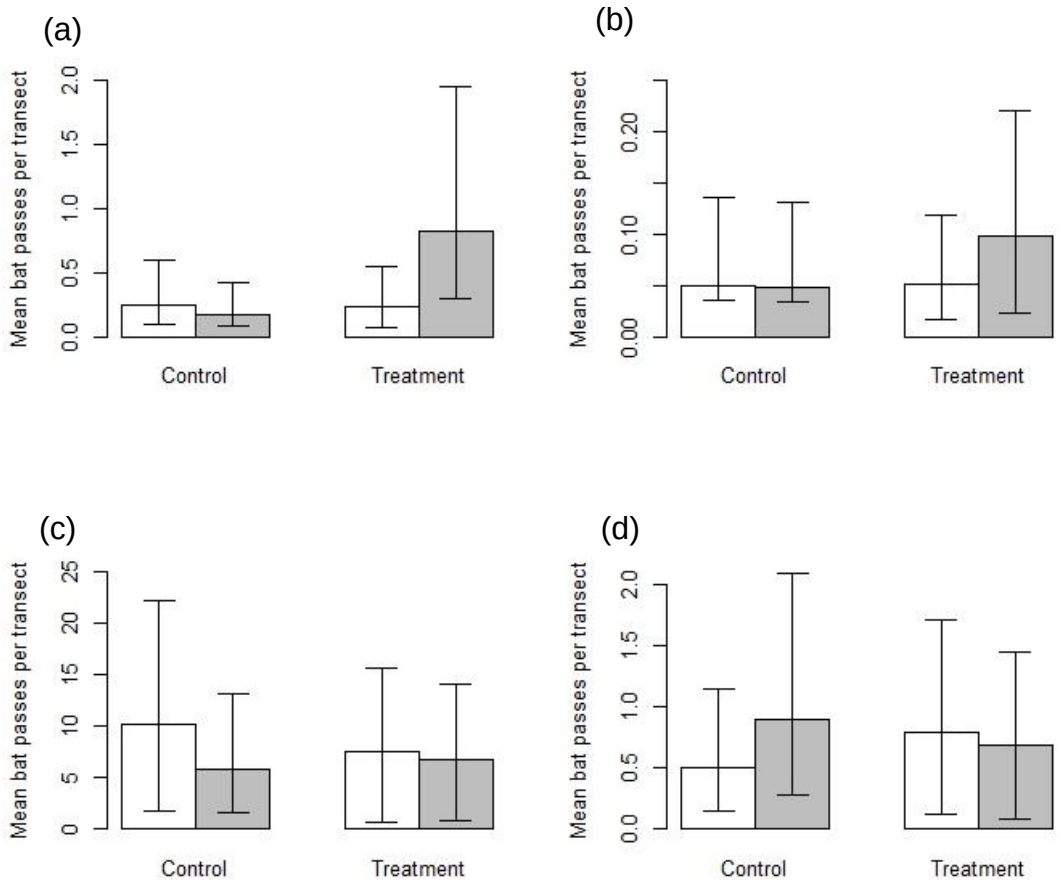


Figure 5.2 Means +/- 95% CI of raw data across all transects for (a) *N. noctula*, (b) *Myotis spp*., (c) *P. pipistrellus* and (d) *P. pygmaeus*. White bars indicate the 2013 surveys and grey bars the 2014 surveys where part-night lighting was operational at treatment sites.

Analysis of the subgroup of sites that changed to part-night lighting showed that there was an interaction between the period of the night and the lighting regime for *N. noctula* (χ^2 = 15.71, *d.f.* = 1, *p*<0.001) and *P. pygmaeus* (χ^2 = 7.99, *d.f.* = 1, *p*<0.005) bat passes. Both *N. noctula* and *P. pygmaeus* had more bat passes during P3 in the dark surveys compared with lit surveys (Figure 5.3c and Figure 5.3d respectively). During P4, there were equal numbers of bat passes of *N. noctula* in both lit and dark surveys but fewer bat passes of *P. pygmaeus* in the dark surveys. Part-night lighting had significantly less *P. pipistrellus* activity (χ^2 = 12.77, *d.f.* = 1, *p*<0.001, Figure 5.2(b)) than lit surveys and the

survey period of the night had a significant effect on activity (χ^2 = 330.42, *d.f.* = 3, *p*<0.001, Figure 5.2(a)). There was no significant difference in *Myotis spp.* bat passes between either lighting regimes or period of the night.

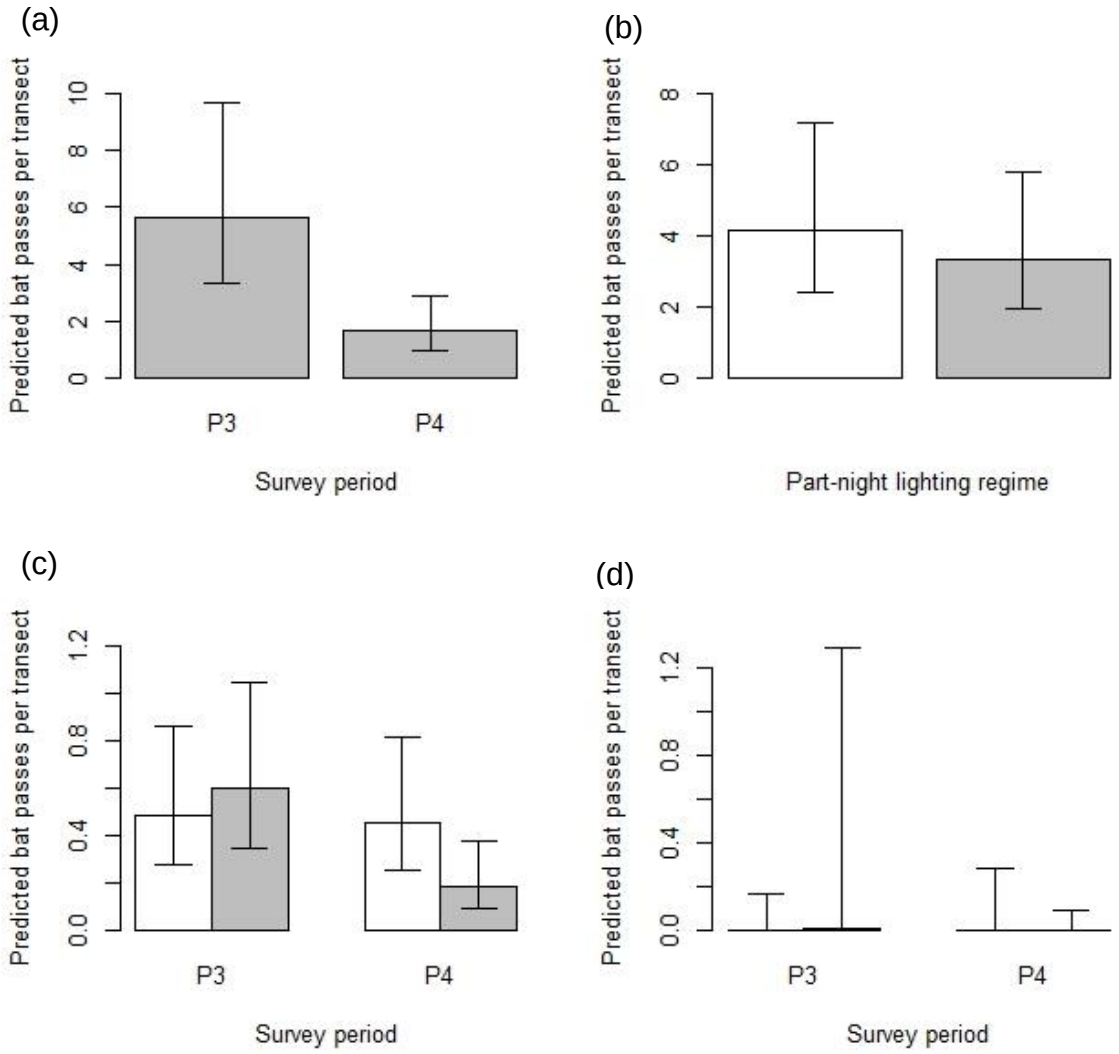


Figure 5.3 Predicted values across sites and transect repeats +/- 95% CI at treatment sites during the P3 and P4 survey periods for (a) *P. pipistrellus*, (b) *P. pipistrellus* for lit and dark surveys, (c) *P. pygmaeus* and (d) *N. noctula*. Values under lit conditions are shown in white and dark conditions are shown in grey.

5.5 Discussion

With artificial nighttime lighting increasing at an estimated rate of 6% per annum (Hölker *et al.* 2010b), there is an urgent need to address and evaluate mitigation for its impacts on the environment. It may be argued that part-night lighting provides a compromise by limiting the impacts of street lighting on wildlife whilst still meeting safety and crime reduction requirements for people. Here we show that part-night lighting compared with full-night lighting may be helpful to some bat species such as *N. noctula*, increasing their activity, but it also decreases activity for *P. pipistrellus*.

Insectivorous bat species can broadly be split in to two groups: species that take advantage of the insects around street lights and actively foraging there (Rydell 1992) and those that avoid lights. Light-avoiding bats tend to have characteristics such as slow flight speed and a gleaning foraging strategy whilst light-tolerant bats fly faster and aerially hawk their prey (Table 1.1; Jones & Rydell 1994). For light-avoiding bat species, such as *Myotis spp.* and *R. hipposideros*, a switch from full-night lighting to part-night lighting should open areas for use during the hours when the lights are off, and so increase numbers of bat passes. For bat species that forage around street lights, such as *Pipistrellus spp.* and *N. noctula*, a reduction in the hours of lighting would be expected to reduce foraging opportunities and decrease the activity indices of these species.

Consistent with these hypotheses, following a reduction in hours of lighting from full-night lighting to part-night lighting, there was a reduction in numbers of *P. pipistrellus* passes recorded (as also seen in Azam *et al.* 2015). There was also, however, an increase

in *P. pygmaeus* and it is unclear why there might be a difference in response to light between species that have similar morphology, flight patterns and foraging strategies. This is consistent with our large-scale observational research at paired light and dark locations, where we have previously found that whilst there is a slight elevation of activity recorded in lit areas for *P. pipistrellus*, this relationship was not apparent for *P. pygmaeus* (Mathews *et al.* 2015, using the data collected in Chapter 3 with additional species analysed).

Following the conversion to part-night lighting, we also found more *N. noctula* bat passes. *N. noctula* is a fast flying bat species (Jones & Rydell 1994) with an aerial hawking foraging strategy (Jones 1995), known to exploit insects attracted to street lamps (Rydell 1992) and so again it is unclear why the reduction in street lighting should have this effect. In an experimental set up of part-night lighting, Azam *et al.* (2015) found conflicting results to those reported here, with more *N. noctula* being recorded when part night-lighting was implemented, but also fewer *N. noctula* when reducing the amount of lighting from part-night lighting to no light. In our study there were low numbers of *N. noctula* and large confidence intervals in predicted values and so the findings should be taken with caution.

Most street lights in Devon, and all the street lights studied here are high-pressure sodium (HPS) vapour lamps. Street lights with different spectra affect bat and bat prey species activity to varying degrees (Lacoeuihe *et al.* 2014, Mathews *et al*. 2015), with broader spectrum lighting (especially those with UV emissions) having more of an effect than narrow spectrum lighting (e.g. see Stone *et al.* 2015b). HPS lamps do not emit much short wavelength lighting compared with, for example, metal halide and so the behaviour of bats around HPS lamps would be expected to be more similar to a dark environment than

around mercury vapour lamps. It may therefore be more of a benefit to apply part-night lighting around more broad spectrum lighting compared with HPS lamps.

A factor which could explain why there was only a small impact of part-night lighting on bat activity is the timing of part-night lighting schemes. The scheme studied here has a switch-off time for street lights in the summer between 1–2 am. Some of the most abundant bat species have a bimodal activity peak around sunset and sunrise with most activity occurring before 11 pm and so part-night lighting schemes are not at the same time as the range of activity for bats (Chapter 4). In this study, the largest number of bat passes for *P. pipistrellus*, *P. pygmaeus* and *N. noctula* occurred during P2 (between sunset and the onset of part-night lighting), meaning most activity was exposed to a street lit environment. Part-night lighting may be more effective to mitigate the impacts on wildlife if it were switched off around sunset and sunrise, however this is quite unlikely to be implemented as it is when most people are using the roads.

The methods for acoustic monitoring in Chapters 3 and 4 were not possible in this study the large number of detectors used in Chapters 3 and 4 were being used on another project. This meant that instead of using multiple point samples at a site, a transect sampling protocol was adopted. A limitation of the transect sampling protocol was that it was only possible to survey each town for one night in each year as additional nights would increase field costs, which is not a limitation for static detectors. However, an advantage of the transect sampling protocol compared with point samples is that point samples can by chance be placed in locations that are not representative of how bats use the wider area you are trying to capture. Therefore, it was necessary to have large numbers of detectors

deployed in Chapters 3 and 4. If point samples were used in this study, it would be wise to place multiple point samples across towns however transect survey multiple locations during a single transect.

Our study demonstrates that although part-night lighting schemes may not be operational during peak bat activity, part-night lighting does alter bat activity compared with full-night lighting. For some species, the reduction in nighttime lighting reduces activity whilst for others it increases activity. Part-night lighting is likely to be implemented to save energy and money but caution should be taken in using it as an effective mitigation to the impacts of street lighting on bats.

Chapter 6: Discussion

Thesis PP 115–123

6.1 Overview

Artificial lighting at night is a growing ecological concern. In this thesis, I have shown that nighttime lighting has differing impacts for different bat species, with some species being highly sensitive to street lighting. As a mitigation option, restricting the duration of artificial light at night through part-night lighting can have limited but marked effects on bat activity. The results found here will help practitioners in the understanding of how street lights impact bats but also what mitigation may be effective.

6.2 Discussion of key findings

6.2.1 Roost exposure to artificial lighting

To quantify levels of artificial light around U.K. bat species' roosts, I carried out a landscape-level assessment of light pollution using satellite imagery. Previous studies have often focused on point sampling around street lights, however bats are highly mobile and their activity patterns are not based around single point locations. It is clear from previous studies that street lighting can reduce activity for some bat species and provide foraging opportunities for others, however it was not clear how much artificial lighting there was in the landscapes around bat roosts and therefore how much of a problem lighting is. In Chapter 2 I analysed light levels around maternity roosts for multiple species, which is the first study of its type.

Here I demonstrated that bat roosts have higher mean light values in the landscapes around their roosts compared with random locations, with significant differences for *P. pipistrellus*, *P. pygmaeus* and *P. auritus.* This is of interest as it suggests bats may prioritise

characteristics other than light when determining where to roost. However, it is important to note that the data used for this analysis is biased towards roosts found in houses rather than trees, caves or other roosting sites and so may not be representative of the whole population. These other roost sites are likely to have darker light profiles as areas with higher housing density will have more street lights and so further assessments of these roosts should be done. The random locations used in this analysis were not constrained by requiring a building to be in the centre of the buffer zone explored which may of the roosts in the NBMP are. An alternative approach to random sampling would be to strategically sample areas to make the roosts and random locations more comparable. Some features of buildings make them more likely for bats to roost in them such as hanging wall tiles and access to roof voids. There was not a dataset available which could represent all of these features and so these analyses were kept relatively simple. Further analyses could constrain random locations to buildings with these building features incorporated.

Although bats do not appear to choose to roost in as dark as that are available in their distributions, there were significant differences in light profiles between species. This suggests that there is an element of preference for light levels around roosts. Bat species that are known to forage around street lights had higher light levels around roosts than bat species known to avoid street lit areas. Efforts should therefore be made to retain dark landscapes especially around bat roosts of species known to avoid street lit areas (Table 1.1). This is especially the case as large roosts were found in dark areas. There are limits with this interpretation, however, as factors which are likely to affect roost size, are correlated with light levels (e.g. woodland cover, housing density) and were not assessed in this analysis. This is further work that should be done and indeed assessing the population

level effects of street lighting on bats was highlighted as a research priority by Stone *et al.* (2015a).

The analysis carried out in Chapter 2 of light levels across roost sustenance and home ranges was done at a coarse scale and may not represent accurately how light or dark a bat perceives the landscape to be. Each home range and sustenance zone was given one value for average light levels from satellite images. There are two problems with this. Firstly, satellite images detect light that is reflected upwards of light sources and bats typically fly below this height. To collect data on light levels at bat height, data could be collected using car mounted sensors (as done in Chapter 3), however this would be impractical for the large number of roosts and areas studied in Chapter 2. An alternative is to predict light levels from street lamp locations. This would also help address a second issue with the satellite data used in Chapter 2. With advances developing in drone technology, it may be possible to use drones to measure light levels at the height of bat flight. The second issue is that two sites could have the same average light levels across the area but very different levels of illumination along commuting paths. With finer scale data, assessments would be possible to identify roosts with high levels of dark connections and those without, which would be useful for management and planning. This finer scale assessment would also potentially allow identification of where roost illumination occurs over time, which was either non-existent or undetected in the analysis presented in Chapter 2.

6.2.2 The greater horseshoe bat

Of the seven bat species assessed in Chapter 2, *R. ferrumequinum* had the lowest number of maternity roosts and is generally understudied with regards to street lighting (see

Table 1.1). To my knowledge, there are no published data on what the impacts of street lighting on *R. ferrumequinum* and so the data presented in Chapter 3 is the first study to evaluate this relationship for this species. *R. ferrumequinum* has a high conservation status across Europe (listed under Appendix II of the European Habitats Directive, 1992/42/EEC) and is in a genus of light avoiding bats and so evidence on the impacts of street lighting on its activity is crucial for management. A common problem with many observational studies on the impacts of street lighting on bats is that locations with street lights in them tend to have very different habitat characteristics to dark locations. Street lit areas are found in more urban areas than dark locations and so have poorer habitat (e.g. see Avila-Flores & Fenton 2005; Rydell 1992). The implications of this is that many studies may be representing the impacts of street lighting and poor habitat quality on bat activity. To overcome this, the study design in Chapter 3 paired street lit and dark locations in similar habitats to have equal representation of habitat quality in each lighting condition. The results presented in this thesis reveal that *R. ferrumequinum* is light intolerant and will avoid street lit areas, even where good habitat is present. In addition, A and B roads had significantly less bat passes than minor roads, a result not published with any bat species before. These two findings have direct management implications in that sensitive areas around *R. ferrumequinum* maternity roosts should avoid street lighting and busy roads.

On exploring other habitat characteristics in Chapter 3, there appeared to be some interactions between habitat characteristics and street light levels which were not significant when modelled. With larger datasets, it may be possible to have a better understanding on how habitat characteristics interact with street light levels. As *R. ferrumequinum* is rare in the landscape and has high frequency calls which are hard to detect on a bat detector

(Adams *et al.* 2012), this analysis could initially be carried out on more common species. These findings would be useful to identify areas of the landscape that should avoid being lit.

6.2.3 Part-night lighting

Part-night lighting is often seen as a popular green option for street lighting, however the agenda behind many part-night lighting schemes is set primarily to save money, with human requirements in mind. The large dataset collected for Chapter 3 allowed for further exploration of the data in the context of part-night lighting to answer the question of do part-night lighting schemes capture peaks in activity for wild animals? The analysis in Chapter 4 revealed that *R. ferrumequinum* has a large primary peak in activity within the first hour after sunset followed by a smaller secondary peak before sunrise. Indeed, the majority of bat activity occurs before 11pm and so common part-night lighting schemes that switch off street lights around 2am are not likely to capture large proportions of bat activity. These results should however be taken in the context of this study; - the species and particularly the time of year that was studied. Following the birth of young in the summer, bats may adapt a less bimodal activity pattern with more constant activity through the night to feed young (Catto *et al.* 1995). With less bimodal activity, part-night lighting may affect bat activity to greater effect than suggested in Chapter 4. This research was the first published paper assessing part-night lighting and its impacts on wildlife.

Although part-night lighting schemes are not designed with bats in mind, many schemes were being implemented across Europe with little information on the likely implications for wildlife. This is a common problem with street lighting in that technological advances lead to rapid changes with unknown consequences. The before-and-after study in Chapter 5 took

advantage of the natural experiment carried out by Devon County Council. At a similar time, Azam *et al.* (2015) conducted an experimental set up of part-night lighting mimicking schemes in France (Azam *et al*. 2015). Within my study, following a conversion from full-night lighting to part-night lighting, there was a significant reduction in *P. pipistrellus* bat passes and a significant increase for *P. pygmaeus* and *N. noctula*. The results found here should be taken with caution, as the sample size was low and recorded bat passes for *P. pygmaeus* and *N. noctula* were low. In Azam *et al.* (2015) there are also conflicting results between different changes to lighting regimes, for instance with some significant differences in bat passes observed when part-night lighting was compared with no light but no observed differences comparing part-night lighting with full night lighting. These results may be a combination of low sample size and due to the street light type studied. Both my study in Chapter 5 and Azam *et al.* (215) were based on High Pressure Sodium lamps, which does not emit UV and so does not have as large of an impact on bats and insects as lamps that emit UV.

Part-night lighting could be developed further then the studies described here. There are many different part-night lighting scenarios that could be possible for instance limiting the duration of lighting to times of the night where bat activity is low, or using motion sensors to limit the use of lighting. Different scenarios such as these should be explored to better understand how limiting the duration of lighting can be used as a mitigation to light pollution.

6.3 Concluding remarks

With street lighting already dominating urban areas and lighting technologies rapidly evolving, research on street lighting is lagging compared with what is required for effective

management (Hölker *et al.* 2010b). Currently ecologists must use their best judgement rather than empirical evidence to select lighting schemes to minimize impacts on bats. In 2007, a EUROBATS Intersessional Working Group was set up for light pollution and in 2016 this working group met to discuss a formal EUROBATS report on light pollution. This offers an international platform to raise the issues of artificial lighting for bats. Within the U.K., although there is legislation which can apply to light pollution, this could be developed further. In 2016 there was a petition put forward to the U.K. government calling for artificial light at night to be acknowledged as a pollutant and have appropriate legislation put in place. With growing evidence mounting on the ecological impacts of light pollution, under the current political climate, we can only hope that experts will not be ignored and evidence will lead to environmental protection.

References

Adams, A. M., Jantzen, M. K., Hamilton, R. M., Fenton, M. B. (2012) Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution*, 3, 992–998.

Alberti, M. (2005) The effects of urban patterns on ecosystem function. *International Regional Science Review*, 28, 168–192.

Arlettaz, R., Godat, S., Meyer, H. (2000) Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biological Conservation*, 93, 55–60.

Arroyo-Solís, A., Castillo, J. M., Figueroa, E., López-Sánchez, J. L., Slabbekoorn, H. (2013) Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *Journal of Avian Biology*, 44, 288–296.

Ashrafi, S., Rutishauser, M., Ecker, K., Obrist, M. K., Arlettaz, R., Bontadina, F. (2013) Habitat selection of three cryptic *Plecotus* bat species in the European Alps reveals contrasting implications for conservation. *Biodiversity and Conservation*, 22, 2751–2766.

Avila-Flores, R. Fenton, M. B. (2005) Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, 86, 1193–1204.

Azam, C., Kerbirious, C., Vernet, A., Julien, J-F., Bas, Y., Plichard, L., Maratrat, J., Le Viol, I. (2015) Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? *Global Change Biology*, 21, 4333–4341.

Baker, J. (1990) Toad aggregations under street lamps. *British Herpetological Society Bulletin*, 31, 26–27.

Bedrosian, T.A., Fonken, L.K., Walton, J.C., Haim, A. & Nelson, R.J. (2011) Dim light at night provokes depression-like behaviors and reduces CA1 dendritic spine density in female hamsters. *Psychoneuroendocrinology* 36, 1062–1069.

Barlow, K. E., Briggs, P. A., Haysom, K. A., Hutson, A. M., Lechiara, N. L., Racey, P. A., Walsh, A. L., Langton, S. D. (2015) Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation*, 182, 14–26.

Becker A., Whitfield A.K., Cowley P.D., Järnegren J., Næsje T.F. (2013) Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary associated fishes. *Journal of Applied Ecology,* 50, 43–50.

Beier, P. (1995) Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management*, 59, 228–237.

Bennett, V.J., Sparks, D.W. & Zollner, P.A. (2013) Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape Ecology*, 28, 979–991.

Bennett, V.J. & Zurcher, A.A. (2013) When corridors collide: Road-related disturbance in commuting bats. *The Journal of Wildlife Management*, 77, 93–101.

Bennie J., Davies, T. W., Duffy, J. P., Inger, R., Gaston, K. J. (2014a) Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Scientific Reports*, 4, 3789.

Bennie, J., Davies, T. W., Inger, R., Gaston, K. (2014b) Mapping artificial lightscapes for ecological studies. *Methods in Ecology and Evolution*, 5, 534–540.

Bennie, J.J., Duffy, J.P., Inger, R. & Gaston, K.J. (2014c) Biogeography of time partitioning in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13727–13732.

Bennie, J., Davies, T.W., Cruse, D., Inger, R. & Gaston, K.J. (2015) Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 370, 20140131.

Billington, G. (2002) Radio Tracking Study of Greater Horseshoe Bats at Chudleigh Caves and Woods Site of Special Scientific Interest. English Nature Research Reports, Peterborough.

Billington, G. (2003) Radio Tracking Study of Greater Horseshoe Bats at Buckfastleigh Caves Site of Special Scientific Interest. English Nature Research Reports, Peterborough.

Bird B.L., Branch L.C., Miller D.L. (2004) Effects of coastal lighting on foraging behavior of beach mice. *Conservation Biology*, 18, 1435–1439.

Blake, D., Hutson, A. M., Racey, P. A., Rydell, J., Speakman, J. R. (1994) Use of lamplit roads by foraging bats in southern England. *Journal of Zoology*, 234, 453–462.

Boldogh, S., Dobrosi, D. & Samu, P. (2007) The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica*, 9, 527–534.

Bontadina, F. (2002) *Conservation ecology in the horseshoe bats Rhinolophus ferrumequinum and Rhinolophus hipposideros.* PhD thesis. University of Bern.

Bontadina, F., Schofield, H., Naef-Daenzer, B. (2002) Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *Journal of Zoology*, 258, 281–290.

Boughey, K. L., Lake, I. R., Haysom, K. A., Dolman, P. M. (2011) Effects of landscape-scale broadleaved woodland configuration and extent on roost locations for six bat species across the UK. *Biological Conservation*, 144, 2300–2310.

Bullock, D.J., Combes, B.A., Eales, L.A. & Pritchard, J.S. (1987) Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrettus*). *Journal of Zoology*, 211, 267–274.

Catto, C. M. C., Hutson, A. M., Racey, P. A., Stephenson, P. J. (1996) Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology*, 238, 623–633.

Catto, C.M.C., Racey, P.A. & Stephenson, P.J. (1995) Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, 235, 635–644.

Cinzano, P., Falchi, F., Elvidge, C. D. (2001) The first World Atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, 328, 689–707.

Costanza R. (1997) The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260.

Crawley, M. (2007) The R Book. John Wiley & Sons, Chichester, England.

Da Silva, A., Valcu, M., Kempenaers, B. (2015) Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 370: 20140126.

Davidson-Watts, I., Walls, S., Jones, G. (2006) Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biological Conservation*, 133, 118–127.

Davies, T. W., Bennie, J., Gaston, K. J. (2012) Street lighting changes the composition of invertebrate communities. *Biology Letters*, 8, 764–767.

Davies, T. W. Bennie, J., Cruse, D., Blumgart, D., Inger, R., Gaston, K. J. (2017) Multiple night-time light-emitting diode lighting strategies impact grassland invertebrate assemblages. *Global Change Biology*, 23, 2641–2648.

Davies, T.W., Duffy, J.P., Bennie, J. & Gaston, K.J. (2014) The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment*, 12, 347–355.

Decoursey, G., Decoursey, P. J. (1964) Adaptive aspects of activity rhythms in bats. *Biological Bulletin*, 126, 14–27.

Delgado, M. J., Gutiérrez, P., Alonso-Bedate, M. (1987) Melatonin and photoperiod alter growth and larval development in *Xenopus laevis* tadpoles. *Comparative Biochemistry and Physiology*, 86A, 417–421.

Department for Transport (2012) Guidance on Road Classification and the Primary Route Network, London.

Dietz, M., Pir, J. B., Hillen. J. (2013) Does the survival of greater horseshoe bats and Geoffroy's bats in Western Europe depend on traditional cultural landscapes? *Biodiversity and Conservatio*n, 22, 3007–3025.

Dominoni, D., Quetting, M., Partecke, J. (2013) Artificial light at night advances avian reproductive physiology. *Proceedings of the Royal Society B: Biological Sciences*, 280: 20123017.

Downs, N. C., Beaton, V., Guest, J., Polanski, J. R., Robinson, S. L., Racey P. A. (2003) The effects of illuminating the roost entrance on the emergence behaviour of *Pipistrellus pygmaeus. Biological Conservation*, 111, 247–252.

Duvergé, P.L., Jones, G., Rydell, J. & Ransome, R.D. (2000) Functional significance of emergence timing in bats. *Ecography*, 23, 32–40.

Dwyer, R. G., Bearhop, S., Campbell, H. A., Bryant, D. M. (2013) Shedding light on light: benefits of anthropogenic illumination to a nocturnally foraging shorebird. *The Journal of Animal Ecology*, 82, 478–485.

Elvidge, C. D., Imhoff, M. L., Baugh, K. E., Hobson, V. R., Nelson, I., Safran, J., Tuttle, B. T. (2001) Night-time lights of the world: 1994-1995*. ISPRS Journal of Photogrammetry and Remote Sensing*, 56, 81–99.

Entwistle, A., Racey, P., Speakman, J. (1996) Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 351, 921–931.

Evans W.R., Akashi Y., Altman N.S., Manville II A.M. (2007) Response of night-migrating songbirds in cloud to colored and flashing light. *North America Birds*, 60, 476–488.

Falchi, F., Cinzano, P., Elvidge, C.D., Keith, D.M., Haim, A. (2011) Limiting the impact of light pollution on human health, environment and stellar visibility. *Journal of Environmental Management*, 92, 2714–2722.

Fensome, A.G. Mathews, F. (2016) Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review*.46, 311–323.

Fenton, M. B. (1970) A technique for monitoring bat activity with results obtained from different environments in southern Ontario. *Candian Journal of Zoology*, 48, 847–851.

Ferraro, P. J., Kiss, A. (2002) Direct payments to conserve biodiversity. *Science*, 298, 1718–1719.

Fonderflick, J., Azam, C., Brochier, C., Cosson, E. & Quékenborn, D. (2015) Testing the relevance of using spatial modeling to predict foraging habitat suitability around bat maternity: a case study in Mediterranean landscape. *Biological Conservation*, 192, 120–129.

Froidevaux, J. S. P., Boughey, K. L., Barlow, K. E. Jones, G. (2017) Factors driving population recovery of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the UK: Implications for conservation. *Biodiversity and Conservation*, 26, 1601–1621.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, 75, 1252–1258.Gaston, K.J. (ed.) (2010) *Urban ecology*. Cambridge University Press, Cambridge.

Gaston, K.J. (ed.) (2010) *Urban ecology*. Cambridge University Press, Cambridge.

Gaston, K.J. (2013) A green light for efficiency. *Nature,* 497, 560–561.

Gaston, K.J., Bennie, J., Davies, T.W. & Hopkins, J. (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological reviews of the Cambridge Philosophical Society*, 88, 912–927.

Gaston, K. J., Bennie, J. (2014) Demographic effects of artificial nighttime lighting on animal populations. *Environmental Reviews,* 22, 323–330.

Gaston, K. J., Davies, T. W., Bennie, J., Hopkins, J. (2012) Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, 49, 1256–1266.

Gaston, K.J., Duffy, J.P., Gaston, S., Bennie, J. & Davies, T.W. (2014) Human alteration of natural light cycles: causes and ecological consequences. *Oecologia,* 176, 917–931.

Gaston, K. J., Duffy, J., Bennie, J. (2015a) Quantifying the erosion of natural darkness in the global protected area system. *Conservation Biology*, 29, 1132–1141.

Gaston, K.J., Gaston, S., Bennie, J. & Hopkins, J. (2014) Benefits and costs of artificial nighttime lighting of the environment. *Environmental Reviews*, 22, 1–10.

Gaston, K.J., Visser, M.E. & Hölker, F. (2015b) The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 370, 20140133.

Geggie, J. F., Fenton M. B. (1985) A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology*, 63, 263–266.

Grimm, N. B., Feath, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., Briggs J. M. (2008) Global change and the ecology of cities. *Science*, 319, 756−760.

Hale J.D., Davies, G., Fairbrass, A.J., Matthews, T.J., Rogers, C.D.F. & Sadler, J.P. (2013) Mapping lightscapes: spatial patterning of artificial lighting in an urban landscape. *PLoS ONE*, 8, e61460.

Hale, J.D., Fairbrass, A., J., Matthews, T. J., Davies, G., Sadler, J. P. (2015) The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Global Change Biology*, 21, 2467–2478.

Hayes, J. (1997) Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy,* 78, 514–524.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., Hanel, A., Kappeler, P. M., Volter, S., Schwope, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C., Tockner, K. (2010a) The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society*, 15, 13.

Hölker, F., Wolter, C., Perkin, E. K., Tockner, K., (2010b) Light pollution as a biodiversity threat. *Trends in Ecology & Evolution*. 25, 681–682.

Holzhaider, J., Kriner, E., Rudolph, B., Zahn, A. (2002) Radio-tracking a lesser horseshoe bat (*Rhinolophus hipposideros*) in Bavaria: an experiment to locate roosts and foraging sites. *Myotis*, 40, 47–54.

Imhoff, M.L., Lawrence, W.T., Stutzer, D.C. & Elvidge, C.D. (1997) A technique for using composite DMSP/OLS ‘city lights’ satellite data to map urban area. *Remote Sensing of Environment*, 61, 361–370.

Inger, R., Bennie, J., Davies, T. W., Gaston, K. J. (2014) Potential biological and ecological effects of flickering artificial light. *PLoS ONE*, e98631.

IUCN (International Union for Conservation of Nature) (2008a) *Eptesicus serotinus*. In: IUCN 2014. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 26 August 2014.

IUCN (International Union for Conservation of Nature) (2008b) *Myotis nattereri*. In: IUCN 2008. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 26 August 2014.

IUCN (International Union for Conservation of Nature) (2008c) *Pipistrellus pipistrellus*. In: IUCN 2008. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 26 August 2014.

IUCN (International Union for Conservation of Nature) (2008d) *Pipistrellus pygmaeus*. In: IUCN 2008. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 26 August 2014.

IUCN (International Union for Conservation of Nature) (2008e) *Plecotus auritus*. In: IUCN 2008. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 26 August 2014.

IUCN (International Union for Conservation of Nature) (2008f) *Rhinolophus hipposideros*. In: IUCN 2008. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 7 December 2014.

IUCN (International Union for Conservation of Nature) (2008g) *Rhinolophus ferrumequinum*. In: IUCN 2014. IUCN Red List of Threatened Species. http://www.iucnredlist.org. 27 March 2014.

Joint Nature Conservation Committee (2013) *Third report by the UK under Article 17 on the implementation of the Habitats Directive from January 2007 to December 2012.* Conservation status assessment for: Greater horseshoe bat (*Rhinolophus ferrumequinum*). Peterborough.

Jones, G. (1995) Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. *Journal of Zoology*, 237, 303–312.

Jones J., Francis C.M. (2003) The effects of light characteristics on avian mortality at lighthouses. *Journal of Avian Biology*, 34, 328–333.

Jones, G. Rydell, J. (1994) Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 346, 445–455.

Kamrowski, R. L., Limpus, C., Jones, R., Anderson, S., Hamann, M. (2014) Temporal changes in artificial light exposure of marine turtle nesting areas. *Global Change Biology*, 20, 2437–2449.

Keith, L. H, Telliard, W. A. (1979) Priority pollutants I-a perspective view. *Environmental Science & Technology*, 13, 416–423.

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., Valcu, M. (2010) Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, 20, 1735–1739.

Kitzes, J. & Merenlender, A. (2014) Large roads reduce bat activity across multiple species. *PLoS ONE*, 9, e96341.

Knight, T. (2006) *The use of landscape features and habitats by the lesser horseshoe bat.* PhD thesis. University of Bristol.

Korine, C., Pinshow, B. (2004) Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev Desert. *Journal of Zoology*, 262, 187–196.

Kronfeld-Schor, N., Dominoni, D., de la Iglesia, H., Levy, O., Herzog, E. D., Dayan T., Helfrich-Forster, C. (2013) Chronobiology by moonlight. *Proceedings of The Royal Society B: Biological Sciences*, 280: 20123088.

Kyba, C. C. M, Ruhtz, T., Fischer, J., Hölker, F. (2011) Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. *PLoS ONE*, e17307.

Lacoeuilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., Kerbiriou, C. (2014) The influence of low intensities of light pollution on bat communities in a semi-natural context. *PLoS ONE*, 9, e103042.

Laidlaw, G. W. J., Fenton, M. B. (1971) Control of nursery colony populations of bats by artificial light. *The Journal of Wildlife Management*, 35, 843–846.

Larsen, L. & Pedersen, J. (1982) The snapping response of the toad, *Bufo bufo*, towards prey dummies at very low light intensities. *Amphibia-Reptilia*, 2, 321–327.

Le Corre, M., Ollivier, A., Ribes, S. & Jouventin, P. (2002) Light-induced mortality of petrels: a 4-year study from Réunion Island (Indian Ocean). *Biological Conservation*, 105, 93–102.

Lewanzik, D., Voigt, C. C. (2014) Artificial light puts ecosystem services of frugivorous bats at risk. *Journal of Applied Ecology*, 51, 388–394.

Lewanzik, D., Voigt, C. C. (2016) Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *Journal of Applied Ecology*, 54, 264–271.

Lintott, P.R., Bunnefeld, N. & Park, K.J. (2015) Opportunities for improving the foraging potential of urban waterways for bats. *Biological Conservation*, 191, 224–233.

Longcore, T, Rich, C. (2004) Ecological light pollution. *Frontiers in Ecology and the Environment*, 2, 191–198.

Loraeu, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D. A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.

Lundy, M. G., Buckley, D. J., Boston, E. S. M., Scott, David D., Prodöhl, P. A., Marnell, F., Teeling, E. C., Montgomery, I. W. (2012) Behavioural context of multi-scale species distribution models assessed by radio-tracking. *Basic and Applied Ecology*, 13, 188–195.

Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., Langton, S. (2015) Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 370, 20140124.

McAney, C.M. & Fairley, J.S. (1988) Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at summer roosts. *Journal of Zoology*, 216, 325–338.

Mcdonald, R.I., Kareiva, P. & Forman, R.T.T. (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141, 1695–1703.

McKinney, M. L. (2002) Urbanization, biodiversity, and conservation. *Bioscience*, 52, 883–890.

Mickleburgh, S., Hutson, A., Racey, P. (2002) A review of the global conservation status of bats. *Oryx*, 36, 18–34.

Miller M.W. (2006) Apparent effects of light pollution on singing behavior of American robins. *The Condor*, 108, 130–139.

Minnaar, C., Boyles, J. G., Minnaar, I. A., Sole, C. L., Mckechnie, A. E. (2015) Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. *Journal of Applied Ecology*, 52, 522–531.

Moore M.V., Pierce S.M., Walsh H.M., Kvalvik S.K., Lim J.D. (2000) Urban light pollution alters the diel vertical migration of Daphnia. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 27, 779–782.

Motte, G., Libois, R. (2002) Conservation of the lesser horseshoe bat (*Rhinolophus hipposideros* Bechstein, 1800) (Mammalia: Chiroptera) in Belgium. A case study of feeding habitat requirements. *Belgian Journal of Zoology*, 132, 47–52.

Nagelkerke, N.J.D. (1991) A note on a general definition of the coefficient of determination. *Biometrika,* 78, 691–692.

Nakagawa, S., Schielzeth, H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

Navara, K.J. & Nelson, R.J. (2007) The dark side of light at night: physiological, epidemiological, and ecological consequences. *Journal of Pineal Research*, 43, 215–224.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senoir, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., Ingram, D. J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha, D.,

Correia, P., Martin, C. D., Meriri, S., Novosolov, M., Pan, Y., Phillips, H. R. P., Purves, D, W., Robinson, A., Simpson, J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M., Scharlemann, J. P. W., Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

Nicholls, B., Racey, P. A. (2006) Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. *Behavioral Ecology and Sociobiology*, 61, 131–142.

O'Hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution,* 1, 118–122.

Ouyang J. Q., de Jong, M., Hau, M., Visser, M. E., Van Grunsven R. H.A., Spoelstra, K. (2015) Stressful colours: corticosterone concentrations in a free-living songbird vary with the spectral composition of experimental illumination. *Biology Letters*, 11, 20150517.

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., Tockner, K. (2011) The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere*, 2, Article 122, 1–16.

Perkin, E.K., Hölker, F. & Tockner, K. (2014) The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshwater Biology*, 59, 368–377.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., Sexton, J. O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.

Poot H., Ens B.J., Vries H.De, Donners M.A.H., Wernand M.R., Marquenie J.M. (2008) Green light for nocturnally migrating birds. *Ecology and Society*, 13, 47.

Poulin C., Bruyant F., Laprise M.-H., Cockshutt A.M., Vandenhecke J.M.R., Huot Y. (2013) The impact of light pollution on diel changes in the photophysiology of *Microcystis aeruginosa*. *Journal of Plankton Research*, 36, 286–291.

Ransome, R., Hutson, A. (2000) Action Plan for the Conservation of the Greater Horseshoe Bat in Europe (*Rhinolophus Ferrumequinum*), Nature and Council of Europe Publishing, Strasbourg.

Ransome, R.D. & McOwat, T.P. (1994) Birth timing and population-changes in greater horseshoe bat colonies (*Rhinolophus ferrumequinum*) are synchronized by climatic temperature. *Zoological Journal of the Linnean Society*, 112, 337–351.

Razgour, O., Hanmer, J., Jones, G. (2011) Using multi-scale modelling to predict habitat suitability for species of conservation concern: the grey long-eared bat as a case study. *Biological Conservation*, 144, 2992–2930.

RCEP (2009) Artificial Light in the Environment: Royal Commission on Environmental Pollution, The Stationary Office, UK.

Reiter, G., Pölzer, E., Mixanig, H., Bontadina, F., Hüttmeir, U. (2012) Impact of landscape fragmentation on a specialised woodland bat, *Rhinolophus hipposideros*. *Mammalian Biology*, 78, 283–289.

Rich, C., Longcore, T. (2006) Ecological consequences of artificial night lighting. Island Press, Washington DC.

Riley W.D., Bendall B., Ives M.J., Edmonds N.J., Maxwell D.L. (2012) Street lighting disrupts the diel migratory pattern of wild Atlantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture*, 330–333, 74–81.

Riley, W.D., Davison, P.I., Maxwell, D.L. & Bendall, B. (2013) Street lighting delays and disrupts the dispersal of Atlantic salmon (*Salmo salar*) fry. *Biological Conservation*, 158, 140–146.

Robinson, M., Stebbings, R. (1997) Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *Journal of Zoology*, 243, 117–136.

Rodríguez A., Rodríguez B., Curbelo Á. J., Pérez A., Marrero S., Negro J. J. (2012) Factors affecting mortality of shearwaters stranded by light pollution. *Animal Conservation*, 15, 519–526.

Rowse, E. G., Harris, S., Jones, G. (2016) The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights. *PLoS ONE*, 11, e0150884.

Rydell, J. (1991) Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. *Holarctic Ecology*, 14, 203–207.

Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, 6, 744-750.

Rydell, J., Natuschke, G., Theiler, A., Peter, Z., E. (1996) Food habits of the barbastelle bat *Barbastella barbastellus*. *Ecography*, 19, 62–66.

Rydell, J., Racey, P.A., (1995) Street lamps and the feeding ecology of insectivorous bats. *Symposia of the Zoological Society of London*, 67, 291–307.

Russ, J. (2012) British Bat Calls: A Guide to Species Identification, 1st ed. Pelagic Publishing, Exeter.

Russo, D., Cistrone, L., Libralato, N., Korine, C., Jones, G., Ancillotto, L. (2017) Adverse effects of artificial illumination on bat drinking activity. *Animal Conservation*, doi:10.1111/acv.12340.

Russo, D. & Jones, G. (2003) Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography*, 26, 197–209.

Rydell, J. (1991) Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. *Holarctic Ecology*, 14, 203–207.

Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, 6, 744–750.

Rydell, J., Entwistle, A. & Racey, P.A. (1996) Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos*, 76, 243–252.

Salmon M., Witherington B. E. (1995) Artificial lighting and sea- finding by loggerhead hatchlings: evidence for lunar modulation. *Copeia*, 4, 931–938.

Sanders, D., Kehoe, R., Tiley, K., Bennie, J., Cruse, D., Davies, T.W., van Veen, F.J.F. & Gaston, K.J. (2015) Artificial nighttime light changes aphid-parasitoid population dynamics. *Scientific Reports* 5, 15232.

Santos C.D., Miranda A.C., Granadeiro J.P., Lourenco P.M., Saraiva S., Palmeirim J.M. (2010) Effects of artificial illumination on the nocturnal foraging of waders. *Acta Oecologica*, 36, 166–172.

Schaub, A., Ostwald, J. & Siemers, B.M. (2008) Foraging bats avoid noise. *The Journal of Experimental Biology*, 211, 3174–3180.

Schofield, H.W. (1996) The Ecology and Conservation Biology of *Rhinolophus hipposideros*, the Lesser Horseshoe Bat. University of Aberdeen.

Seto, K. C., Güneralpa, B., Hutyra, L. R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 16083–16088.

Shirley, M. D. F., Armitage, V. L., Barden, T. L., Gough, M., Lurz, P. W. W., Oatway, D. E., South, A. B., Rushton, S. P. (2001) Assessing the impact of a music festival on the emergence behaviour of a breeding colony of Daubenton's bats (*Myotis daubentonii*). *Journal of Zoology*, 254, 367−373.

Skalak, S.L., Sherwin, R.E. & Brigham, R.M. (2012) Sampling period, size and duration influence measures of bat species richness from acoustic surveys. *Methods in Ecology and Evolution,* 3, 490–502.

Sleep, D.J.H. & Brigham, R.M. (2003) An experimental test of clutter tolerance in bats. *Journal of Mammalogy*, 84, 216–224.

Smith, P. G. (2000) *Habitat preference, range use and roosting ecology of Natterer's bats (Myotis nattereri) in a grassland-woodland landscape*. PhD thesis. University of Aberdeen.

Somers-Yeates, R., Hodgson, D., Mcgregor, P. K., Spalding, A., ffrench-Constant, R. H. (2013) Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biology Letters*, 9, 20130376.

Spoelstra, K., van Grunsven, R. H. A., Ramakers, J. J. C., Ferguson, K. B., Raap, T., Donners, M., Veenendaal, E. M., Visser, M. E. (2017) Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the Royal Society of London B: Biological Sciences*, 284, 11–15.

Steinbach, R., Perkins, C., Tompson, L., Johnson, S., Armstrong, B., Green, J., Grundy, C., Wilkinson, P., Edwards, P. (2015) The effect of reduced street lighting on road casualties and crime in England and Wales: controlled interrupted time series analysis. *Journal of Epidemiology & Community Health*, 69, 1118–1124.

Stone, E. L., Jones, G., Harris, S. (2009) Street lighting disturbs commuting bats. *Current Biology*, 19, 1123–1127.

Stone, E. L., Jones, G., Harris, S. (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, 18, 2458–2465.

Stone, E. L., Harris, S., Jones, G. (2015a) Impacts of artificial lighting on bats: A review of challenges and solutions. *Mammalian Biology*, 80, 213–219.

Stone, E. L., Wakefield, A., Harris, S., Jones, G. (2015b) The impacts of new street light technologies: experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 370, 20140127.

Stone, E. L., Zeale M. R. K., Newson S. E., Browne W.J., Harris S., Jones G. (2015c) Managing conflict between bats and humans: The response of soprano pipistrelles (*Pipistrellus pygmaeus*) to exclusion from roosts in houses. *PLoS ONE*, 10, e0131825.

Sutherland, W. J., Armstrong-Brown, S., Armsworth, P. R.,Tom, B., Brickland, J., Campbell, C. D., Chamberlain, D. E., Cooke, A. I., Dulvy, N. K., Dusic, N. R., Fitton, M., Freckleton, R. P., Godfray, H. C. J., Grout, N., Harvey, H. J., Hedley, C., Hopkins, J. J., Kift, N. B., Kirby, J., Kunin, W. E., Macdonald, D. W., Marker, B., Naura, M., Neale, A. R., Oliver, T., Osborn, D., Pullin, A. S., Shardlow, M. E., Showler, D., Smith, P. L., Smithers, R. J., Solandt, J.-L., Spencer, J., Spray, C. J., Thomas, C. D., Thompson, J., Webb, S. E., Yalden, D. W., Watkinson, A. R. (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology*, 43, 617–627.

Sutton, P.C. (2003) A scale-adjusted measure of ‘urban sprawl’ using nighttime satellite imagery. *Remote Sensing of Environment,* 86, 353–369.

Svensson, A. M., Rydell, J. (1998) Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera spp*.; Geometridae). *Animal Behaviour*, 55, 223–226.

The British Standards Institution (2012) *Code of practice for the design of road lighting. Part 1: Lighting of roads and public amenity areas*. London.

The Royal Commission on Environmental Pollution. (2009) Artificial light in the environment. TSO, London.

Threlfall, C. G., Law, B., Banks, P. B. (2013) The urban matrix and artificial light restricts the nightly ranging behaviour of Gould's long-eared bat (*Nyctophilus gouldi*). *Austral Ecology*, 38, 921–930.

Titulaer M., Spoelstra K., Lange C.Y.M.J.G., Visser M.E. (2012) Activity patterns during food provisioning are affected by artificial light in free living great tits (*Parus major*). *PLoS ONE*, 7, e37377.

UN (2015) World Urbanization Prospects: The 2014 Revision (ST/ESA/SER.A/366). Available at: http://esa.un.org/unpd/wup/Publications/Files/WUP2014-Report.pdf.

van Geffen, K.G., van Eck, E., de Boer, R.A., van Grunsven, R.H.A., Salis, L., Berendse, F. & Veenendaal, E.M. (2015) Artificial light at night inhibits mating in a geometrid moth. *Insect Conservation and Diversity*, 8, 282–287.

van Geffen, K. G., Groot, A. T., Van Grunsven, R. H.A., Donners, M., Berendse, F., Veenendaal, E. M. (2015) Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecological Entomology*, 40, 401–408.

van Gelder, R. G. (1956) Echo-location failure in migratory bats. *Transactions of the Kansas Academy of Science (1903-),* 59, 220–222.

van Langevelde F., Ettema J. A., Donners M., WallisDeVries M. F., Groenendijk D. (2011) Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144, 2274–2281.

Voigt, C. C., Roeleke, M., Marggraf, L. (2017) Migratory bats respond to artificial green light with positive phototaxis. *PLoS ONE*, 12, e0177748.

Wakefield, A., Stone, E. L., Jones, G., Harris, S. (2015) Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls. *Royal Society Open Science*, 2, 150291.

Walsh, A.L. & Harris, S. (1996) Factors determining the abundance of vespertilionid bats in Britain: geographical, land classes and local habitat relationships. *Journal of Applied Ecology*, 33, 519–529.

Welch D. & Dick R. (2012) International dark-sky efforts. *Journal of the Royal Astronomical Society of Canada*. Special Issue 2012, 22–25.

Zeale, M. R. K., Bennitt, E., Newson, S. E., Packman, C., Browne, W. J., Harris, S., Jones, G., Stone, E. (2016) Mitigating the impact of bats in historic churches: the response of Natterer's bats *Myotis nattereri* to artificial roosts and deterrence. *PLoS ONE*, 11, e0146782.

Zurcher, A.A., Sparks, D.W. & Bennett, V.J. (2010) Why the bat did not cross the road? *Acta Chiropterologica*, 12, 337–340.

Appendices

Appendix Table 2.1 Number of unique roosts per species analysed with full DMSP-OLS, 2012 DMSP-OLS and Suomi-NPP datasets.

Species	Number of roosts		
	DMSP-OLS	2012 DMSP-OLS	Suomi NPP
R. hipposideros	295	185	185
R. ferrumequinum	30	26	26
M. nattereri	90	40	40
Pl. auritus	197	68	68
Pi. pipistrellus	544	231	231
Pi. pygmaeus	401	135	135
E. serotinus	133	34	34

Appendix Table 2.2 Model outputs comparing roost and random location light profiles. *p* <0.05 *, *p* <0.01 **, *p* <0.001 *** For all datasets. RS = Roost sustenance, HR = Home range. There was a significant difference between species for all datasets: DMSP-OLS RS ($F_{6,8674.4}$ = 9.00, p <0.001, $R^2_{GLMM(M)}$ = 0.05, $R^2_{GLMM(C)}$ = 0.99), DMSP-OLS HR ($F_{6,8674.9}$ = 9.54, p <0.001, $R^2_{GLMM(M)}$ = 0.06, $R^2_{GLMM(C)}$ = 0.99), 2012 DMSP-OLS RS ($F_{6,8676}$ = 9.96, p <0.001, adjusted R^2 = 0.05), 2012 DMSP-OLS HR ($F_{6,8676}$ = 10.22, p <0.01, adjusted R^2 = 0.05), Suomi NPP RS ($F_{6,8676}$ = 4.25, p <0.001, adjusted R^2 = 0.02) and Suomi NPP HR ($F_{6,8676}$ = 4.14, p <0.01, adjusted R^2 = 0.02).

Data			F	df	p	$R^2_{GLMM(M)}$	$R^2_{GLMM(C)}$	Adjusted R^2	est
E. serotinus	DMSP-OLS	Full RS	3.06	1, 1131	0.08	0.003	0.991		-2.69
		Full HR	3.38	1, 1131	0.07	0.004	0.996		-2.38
		2012 RS	3.23	1, 1131	0.07			0.002	-2.76
		2012 HR	3.80	1, 1131	0.05			0.003	-2.51
	Suomi	RS	0.68	1, 1131	0.41			-0.0003	0.35
		HR	1.43	1, 1131	0.23			0.0004	0.39
M. nattereri	DMSP-OLS	Full RS	0.06	1, 1088	0.81	6.4E-05	0.99		-0.44
		Full HR	1.16	1, 1088	0.28	0.001	0.995		-1.75
		2012 RS	0.00	1, 1088	0.98			-0.0009	-0.05
		2012 HR	0.95	1, 1088	0.33			-0.00004	-1.57
	Suomi	RS	2.02	1, 1088	0.16			0.0009	0.89
		HR	0.14	1, 1088	0.71			-0.0008	0.17
P. pipistrellus	DMSP-OLS	Full RS	79.65	1,1542	***	0.052	0.99063		-8.58
		Full HR	81.02	1, 1542	***	0.053	0.99356		-8.14
		2012 RS	82.98	1, 1542	***			0.0505	-8.78
		2012 HR	83.72	1, 1542	***			0.0509	-8.22
	Suomi	RS	10.68	1, 1542	***			0.0062	-0.10
		HR	14.27	1, 1542	***			0.0085	-0.97

P. pygmaeus	DMSP-OLS	Full RS	60.25	1, 1399	***	0.045	0.99065		-7.96
		Full HR	60.05	1, 1399	***	0.045	0.99233		-7.71
		2012 RS	65.01	1, 1399	***			0.0437	-8.27
		2012 HR	65.13	1, 1399	***			0.0438	-8.01
	Suomi	RS	10.33	1, 1399	**			0.0066	-0.93
		HR	10.24	1, 1399	**			0.0066	-0.91
P. auritus	DMSP-OLS	Full RS	9.34	1, 1195	**	0.009	0.98983		-3.81
		Full HR	11.66	1, 1195	***	0.011	0.99253		-4.13
		2012 RS	7.95	1, 1195	**			0.0058	-3.53
		2012 HR	10.63	1, 1195	**			0.0080	-3.94
	Suomi	RS	0.15	1, 1195	0.70			-0.0007	0.14
		HR	0.01	1, 1195	0.91			-0.0008	0.04
R. ferrumequinum	DMSP-OLS	Full RS	1.73	1, 1028	0.19	0.002	0.99253		-2.97
		Full HR	3.11	1, 1028	0.08	0.004	0.99514		-2.92
		2012 RS	1.92	1, 1028	0.17			0.0009	-3.11
		2012 HR	3.13	1, 1028	0.08			0.0021	-2.95
	Suomi	RS	0.32	1, 1028	0.57			-0.0007	0.23
		HR	0.03	1, 1028	0.86			-0.0009	-0.04
R. hipposideros	DMSP-OLS	Full RS	1.27	1, 1293	0.26	0.00111	0.98733		-0.89
		Full HR	0.90	1, 1293	0.34	0.00079	0.99228		-0.66
		2012 RS	0.95	1, 1293	0.33			-0.00004	-0.78
		2012 HR	0.70	1, 1293	0.40			-0.0002	-0.58
	Suomi	RS	0.64	1, 1293	0.42			-0.0003	0.11
		HR	0.12	1, 1293	0.73			-0.0007	0.04

Appendix Table 2.3 Satellite light exposure comparisons between species. For each species, adjusted *P* values are given (where less than 0.1) from models run with DMSP-OLS roost sustenance full dataset values, DMPS-OLS home-range full dataset values, DMSP-OLS roost sustenance 2012 values, DMPS-OLS home-range 2012 values, Suomi-NPP roost sustenance values, and Suomi-NPP home-range values (top to bottom). *P*-values are shown in green where the base species has a larger light value than the comparison species and red where there is a lower value. Significance levels: <0.05 *, <0.01 **, <0.001 ***. There was a significant difference between all species for all models: DMSP-OLS sustenance zone full dataset ($F_{6, 1683.9} = 16.96$, p <0.001, $R^2_{GLMM(M)} = 0.056$, $R^2_{GLMM(C)} = 0.988$), DMSP-OLS home range full dataset ($F_{6, 1680.5} = 17.44$, p <0.001, $R^2_{GLMM(M)} = 0.058$, $R^2_{GLMM(C)} = 0.991$), DMSP-OLS sustenance zone 2012 dataset ($F_{6, 8675.4} = 11.23$, p <0.001, $R^2_{GLMM(M)} = 0.005$, $R^2_{GLMM(C)} = 0.469$), DMSP-OLS home range 2012 dataset ($F_{6, 8671.9} = 12.76$, p <0.001 , $R^2_{GLMM(M)} = 0.005$, $R^2_{GLMM(C)} =0.526$), Suomi sustenance zone ($F_{6, 1673.8} = 7.59$, p <0.001, $R^2_{GLMM(M)} = 0.014$, $R^2_{GLMM(C)} = 0.499$) and Suomi home range ($F_{6, 1673.2} = 4.61$, p = 0.001, $R^2_{GLMM(M)} = 0.008$, $R^2_{GLMM(C)} = 0.556$).

Base species	Comparison species	EPSE	MYNA	PIPI	PIPY	PLAUR	RHFE	RHHI
EPSE		-	*			0.07		***
		-						***
		-			0.06			***
		-			*			***
		-	*					
		-						
MYNA		*	-	***	**			
			-	**	**			
			-	0.08	*			*
			-	***	***			0.05
		*	-					
			-					
PIPI			***	-		***		***
			**	-		***		***
			0.08	-		***	***	***
			*	-		***	***	***
				-		**		*
				-		*		
PIPY			**		-	*		***
			**		-	*		***
		0.06	*		-	***	***	***
		*	**		-	***	***	***
					-	*		
					-	*		
PLAUR		0.07		***	**	-		0.06
				**	**	-		**
				***	***	-		
				***	***	-		

| | | |

Appendix Table 2.4 Significance levels from models predicting roost size by light levels and species.

Dataset	Variable	χ^2	d.f.	p
DMSP-OLS roost sustenance	light	583.51	6	<0.001
	species	56.56	1	<0.001
DMSP-OLS home range	light	580.45	6	<0.001
	species	60.47	1	<0.001
Suomi-NPP roost sustenance	light	140.78	6	<0.001
	species	103360	1	<0.001
Suomi-NPP home range	light	140.63	6	<0.001
	species	103360	1	<0.001

Appendix Table 2.5 Predicted changes in light levels of time by species and region. Significance levels shown p<0.001 ***, p<0.01 ***, p<0.05 *. Where slope estimates are significant, values are highlighted in green for positive trends and red for negative trends.

Variable		DMSP-OLS roost sustenance				DMSP-OLS home range			
		Slope estimate	χ^2	d.f.	p	Slope estimate	χ^2	d.f.	p
Species	*E. serotinus*	-0.004	0.35	1	0.55	0.003	0.29	1	0.59
	M. nattereri	-0.0001	0.00	1	0.99	0.005	0.74	1	0.39
	P. pipistrellus	0.009	7.75	1	**	0.012	22.27	1	***
	P. pygmaeus	0.005	2.01	1	0.16	0.013	17.42	1	***
	P. auritus	0.005	0.86	1	0.35	0.008	3.49	1	0.06
	R. ferrumequinum	-0.0002	0.00	1	0.99	-0.008	0.62	1	0.43
	R. hipposideros	-0.024	18.35	1	***	-0.014	10.45	1	**
Region	East Midlands	-0.015	5.62	1	*	-0.001	0.07	1	0.80
	East of England	-0.050	50.03	1	***	-0.042	56.47	1	***
	Greater London	0.003	0.05	1	0.83	0.002	0.05	1	0.83
	North East	0.092	52.64	1	***	0.089	76.07	1	***
	North West	-0.043	29.31	1	***	-0.041	42.31	1	***
	Scotland	0.020	13.74	1	***	0.021	23.70	1	***
	South East	-0.058	144.33	1	***	-0.052	183.02	1	***
	South West	-0.011	6.35	1	*	-0.008	6.18	1	*
	Wales	0.045	79.40	1	***	0.042	109.03	1	***
	West Midlands	0.039	33.93	1	***	0.035	42.23	1	***
	Yorkshire and The Humber	-0.038	17.53	1	***	-0.016	4.87	1	*

Appendix Table 3.1 Light meter channel wavelength specifications and units.

Channel	Wavelength peak sensitivity (nm)
Lux	NA
UVA	NA
Red	NA
Far red	NA
Channel 1 (violet)	400.1
Channel 2 (blue)	462.9
Channel 3 (green)	532.0
Channel 4 (orange)	590.5

Appendix Table 3.2 Correlation matrix of spectrum readings across detectors and sites. Correlation values above 0.6 are shown in bold.

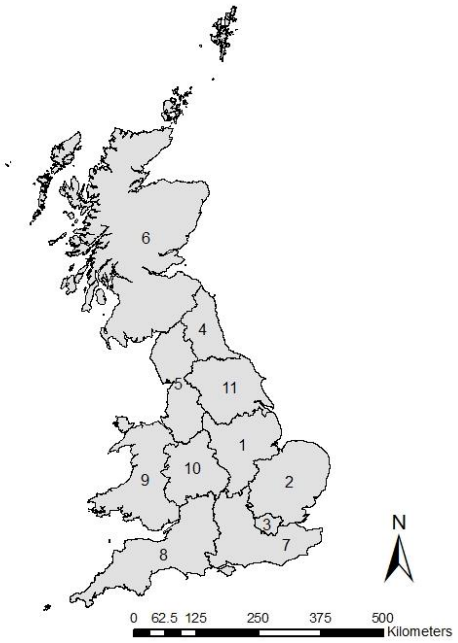
	Lux	UVA	Red	Far red	Chan 1 (violet)	Ch 2 (blue)	Ch 3 (green)	Ch 4 (orange)
Lux	**1.000**	0.085	**0.819**	**0.725**	0.156	0.515	**0.858**	**0.917**
UVA	0.085	**1.000**	0.104	0.155	0.125	0.149	0.140	0.045
Red	**0.819**	0.104	**1.000**	**0.905**	0.143	0.519	**0.784**	**0.697**
Far red	**0.725**	0.155	**0.905**	**1.000**	0.203	0.538	**0.695**	0.589
Ch 1 (violet)	0.156	0.125	0.143	0.203	**1.000**	0.477	0.288	0.181
Ch (blue)	0.515	0.149	0.519	0.538	0.477	**1.000**	**0.679**	0.480
Ch 3 (green)	**0.858**	0.140	**0.784**	**0.695**	0.288	**0.679**	**1.000**	**0.832**
Ch 4 (orange)	**0.917**	0.045	**0.697**	0.589	0.181	0.480	**0.832**	**1.000**

Appendix Table 5.1 Site location and survey night.

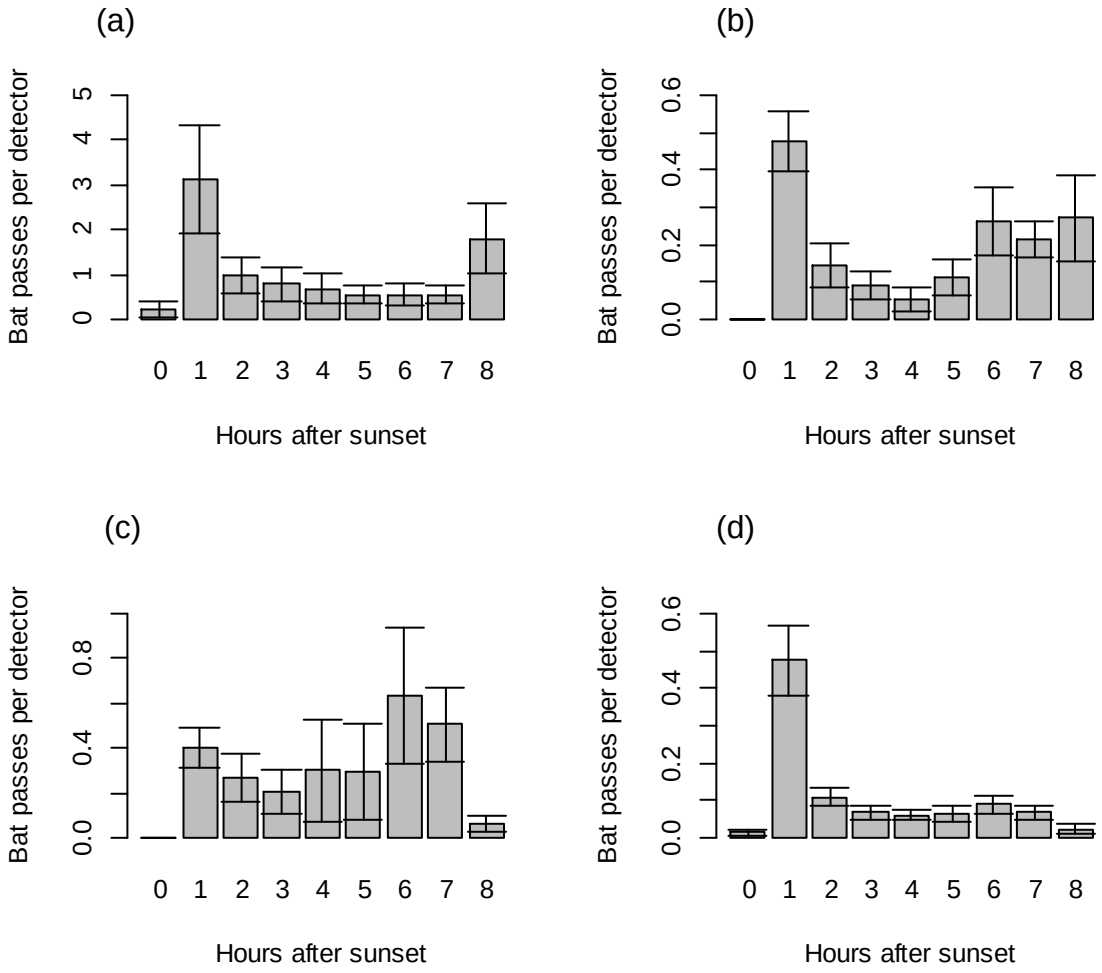
Site type	Town name	Survey night	
		Year 1	Year 2
Treatment	Atherington	09/07/2013	21/07/2014
	Beaford	25/08/2013	12/09/2014
	Bratton Fleming	06/07/2013	01/07/2014
	Cheriton Fitzpaine	01/07/2013	30/06/2014
	Chittlehampton	16/07/2013	22/07/2014
	Combe Martin	12/07/2013	10/07/2014
	Kenton	17/07/2013	30/07/2014
	Kingsteighton	17/09/2013	16/09/2014
	Monkokehampton	16/08/2013	10/09/2014
	Ogwell	05/09/2013	28/08/2014
	Okehampton	26/08/2013	09/09/2014
	Princetown	20/08/2013	11/09/2014
	Rackenford	10/07/2013	03/07/2014
	Swimbridge	11/07/2013	08/07/2014
	Walkhampton	18/08/2013	08/09/2014
	Landkey	21/07/2013	23/07/2014
	Silverton	14/07/2013	11/07/2014
Control	Bishops Nympton	13/07/2013	09/07/2014
	Dolton	23/07/2013	29/07/2014
	Lympstone	22/08/2013	22/08/2014
	Otterton	23/09/2013	17/09/2014

Appendix Table 5.2 Overall bat passes per period across all sites.

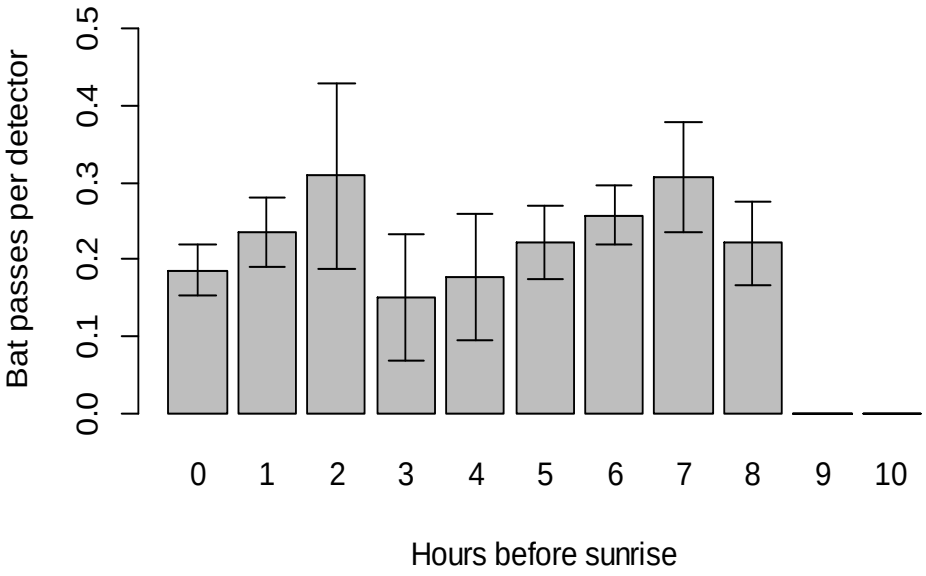
Survey period	*B. barbastellus*	*Myotis spp.*	*N. noctula*	*P. pipistrellus*	*P. pygmaeus*	*R. hipposideros*
P1	0	1	8	140	20	0
P2	0	8	164	1913	181	0
P3	0	12	41	1056	89	2
P4	2	12	10	312	56	0



Appendix Figure 2.1 Civil regions with boundaries. 1: East Midlands, 2: East of England, 3: Greater London Authority, 4: North East, 5: North West, 6: Scotland, 7: South East, 8: South West, 9: Wales, 10: West Midlands and 11: Yorkshire and The Humber.



Appendix Figure 4.1. Mean hourly bat passes (± SE) at subsets of detectors across sites within different distances from the roost: (a) 500 m–1 km, (b) 1–2 km, (c) 2–3 km, and (d) > 3 km.



Appendix Figure 4.2. Mean hourly bat passes (± SE) across sites and detectors.

Acknowledgements

The PhD process can be quite a solitary one, however there have been many people who have helped me through it, to whom I will always be grateful for.

First and foremost, I would like to thank my internal supervisors, Dr Fiona Mathews and Professor Kevin Gaston. I am grateful to have joined Dr Fiona Mathews' research group who carry out research on cutting edge applied British bat conservation research. Fiona has acquired excellent resources for bat research, which were made available to me, meaning I have had levels of equipment which have been quite amazing for a PhD. I am grateful for Fiona's good understanding of study design and statistics, which helped me collect robust datasets with sometimes tricky real world studies. I'd like that thank Kevin for all his help in with writing manuscripts, his clear vision, speedy response and for always making time for my work.

I'd like to thank my funders, Defra, the Department of Environment, Food and Rural Affairs, firstly for putting funding into research on an understudied form of pollution, and secondly for facilitating my research and development. I'd also like to thank additionally funders who allowed me to attend conferences to present my work after my main funding had ended: The British Ecological Society and the University of Exeter's Doctorate College.

I would like to thank The Vincent Wildlife Trust who were collaborators on my project. Dr Henry Schofield, my external supervisors for his expert knowledge

on horseshoes and support throughout my PhD on manuscripts and conference attendance. Without James Baker by my side through a large proportion of my fieldwork, I would have been lost dealing with large numbers of bat detectors I had never used before and fieldwork vehicles that had a nasty habit of breaking down. Before starting my PhD, I had only encountered bats a few times and so the thought of embarking on a PhD focused on bats was quite daunting and so I can't thank Colin Morris enough for allowing me to come with him on many roost visits and bat box checks over the years. These have always been highly enjoyable trips, where Colin has shared his knowledge, experience and jokes freely.

I would like to thank all the external group who have helped me complete my PhD. Firstly, all the members of the Defra steering group meetings. I would also like to thank all the county councils who have given data on street lighting in their area: Devon County Council, Somerset County Council and Wiltshire County Council. I would particularly like to thank Maurizo D'Alesio at Devon County Council for all the help over the years. I would like to thank the Bat Conservation Trust, and particularly the late Kate Barlow for making large datasets on bat roosts available for all of my research group.

My research group have offered me so much help and support, from teaching me new skills, listening to me prepare presentations, and to perhaps most importantly, sharing in struggles together. Over the years, there were also many fieldworkers who joined our research group for varying lengths of time and I'd like to thank everyone who helped me in the field: James Baker, Lee Haley,

Asia Kohyt, Tamara Lumb, Oliver Leader, Euan Tilling, Flo Taylor, Flavio Winkler and Jack Allen.

Finally, I can’t thank all my friends and family enough for support in so many ways. Thank you, Jack, and your family for a huge range of support from helping me prepare for presentations, proof reading documents, lending me a bike for some of my surveys and many more things. I can’t thank Chris enough for taking me into his home during my final year of my PhD, giving me the space to complete my thesis and never asking anything in return.